GROWTH AND DISINTEGRATION OF BIVALVE-DOMINATED PATCH REEFS IN THE UPPER JURASSIC OF SOUTHERN ENGLAND

by FRANZ T. FÜRSICH, TIMOTHY J. PALMER *and* KAY L. GOODYEAR

ABSTRACT. Patch reefs, up to 4 metres high and 8 metres across, grew amongst oolith shoals at the top of the Portland Limestone Formation (Portlandian, Upper Jurassic) on the Isle of Portland, southern England. Principal reef framebuilders, which provided between 55 and 70 per cent of the reef volume, were cementing bivalves, solenoporacean algae, and bryozoans. The remaining pore-space in the reef was filled by sediment, most of which is in the form of a precipitated peloidal cement. The cement lithified the reef while it was still exposed on the sea floor, and was probably precipitated under bacterial control. A diverse accessory fauna of small cementing encrusters and nestlers includes groups such as terebratulid brachiopods and lithistid sponges that have not previously been found in the Portland Limestone. *Serpula* (*Cycloserpula*) *striatissima* sp. nov. and *Carterochaena pulcherrima* gen. et sp. nov. are described. Both the primary organic framework of the reef and the submarine cements were bored by a variety of endoliths, which locally removed as much as 40 per cent of the reef volume. Vacated borings acted as sites for precipitation of further peloidal cement. Borings are well preserved as natural three-dimensional casts in cases where they originally perforated an aragonite substrate which has since dissolved. New taxa of borings consist of *Cunctichnus probans* ichnogen. et ichnosp. nov., *Spirichnus spiralis* ichnogen. et ichnosp. nov., *Talpina bromleyi* ichnosp. nov., and *Entobia cervicornis* ichnosp. nov.

THE Portlandian limestones of Dorset in southern England constitute some of the most closely-scrutinized carbonate sections in the world, given their place in the field-trip itineraries of many educational establishments, commercial operations, and local interest groups. They are excellently developed and exposed on the Isle of Portland in Dorset, southern England (Text-fig. 1), where the topmost Portlandian is developed in an oolitic freestone facies that has traditionally been regarded as England's best building stone for fine quality ashlar and mouldings. Hence there are many good quarry exposures on the island as well as natural outcrops in the cliffs. Notwithstanding their fame, however, the Portland limestones in Dorset have received only a modest amount of scientific attention. Nineteenth and early twentieth century studies described stratigraphical, lithological and palaeontological details (Buckland and De la Beche 1836; Fitton 1836; Blake 1880; Damon 1884; Woodward 1895; Arkell 1947) and the current state of biostratigraphical refinement within the Portlandian Stage has only recently been attained (Wimbledon and Cope 1978; Wimbledon *in* Cope *et al.* 1980). The only modern sedimentological study that deals with depositional processes and environments is that of Townson (1975). Surprisingly, it was not until this work that the spectacular patch reefs that form the subject of this paper were first recognized as a distinct facies. This is probably a reflection of the relative inaccessibility of the Isle of Portland in former times, the very local development of the reef facies in the more northerly part of the island where most of the quarries were concentrated last century, and its former lack of economic value. This study thus sets out to describe the palaeoecology and the sedimentary dynamics of these spectacular but little-known build-ups, whose guild structure shows many similarities with modern, coral-dominated patch-reefs.

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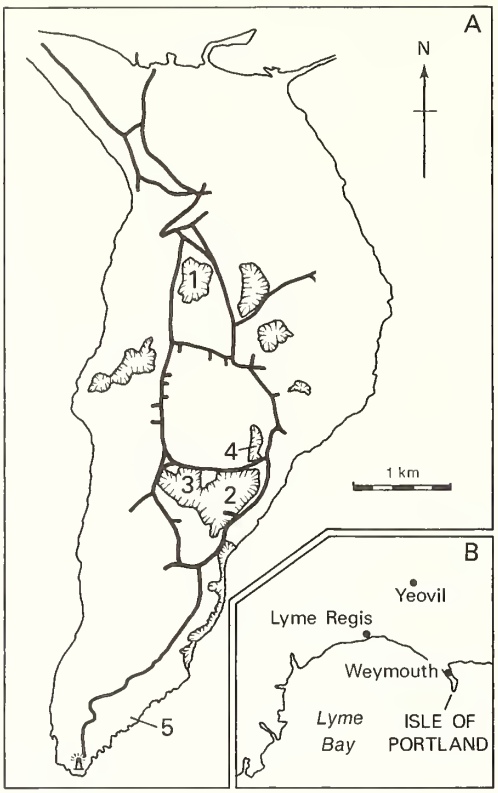


TEXT-FIG. 1. A, sites on the Isle of Portland, Dorset, where patch-reefs have been examined for this study: 1, Inmosthay Quarry; 2, Coombefield Quarry; 3, Suckthumb Quarry; 4, Perryfield Quarry; 5, shore north-east of Portland Bill. B, location of Isle of Portland on the coast of southern England.

STRATIGRAPHICAL AND GEOGRAPHICAL FRAMEWORK

Lithostratigraphy and age

The reefs occur in the top 3 to 4 metres of the Portland Stone, in the upper part of the Portland Freestone Member of Cope *et al.* (1980). Townson (1975) called this unit the Winspit Member of the Portland Limestone Formation, but use of this name has not caught on.

All the individual beds in the upper part of the Portland Stone on Portland (from where nearly all the building stone comes) have individual quarrymen's names which are widely used by geologists, and which have appeared in many earlier geological accounts (e.g. Arkell 1933, 1947). The topmost oolitic grainstone widely becomes fossiliferous towards its top, giving rise to a horizon (not usually more than about 0·7 m thick) called the Roach, which is particularly characterized by preservation of open biomoulds after aragonite. The familiar Roach contains a soft-sediment fauna dominated by high-spired gastropods and infaunal bivalves. At a few localities, the Roach thickens to as much as 4 m at the expense of the rest of the bed and develops the biohermal character that we describe here. The Portland Freestone Member belongs to the Zone of *Titanites anguiformis* (Cope *et al.* 1980).

The Roach Bed in the Portland Quarries is immediately overlain by the palaeosols and thrombolites of the basal Purbeck Limestone Formation (Francis 1986), indicating emergence from the marine, into subaerial and lacustrine conditions.

Patch-reef localities

Renewed interest in natural building materials in the last decade has seen the reopening and expansion of many of the older quarries on Portland, and both small and large examples of the patch-reefs have been exposed and examined by us as quarry walls have receded. The reef facies is

sometimes slabbed and used commercially as a cladding stone on modern buildings, so that large blocks of the native reef rock may sit around in the quarries awaiting sale after the natural outcrop has been quarried away. *In situ* reefs in existing quarry walls can be seen at Inmosthay and Suckthumb Quarries and in the coastal exposure about 1 km northeast of Portland Bill. A very large example was formerly exposed at one of the quarries east of the main road in Easton (D. W. J. Bosence pers. comm.). We have also studied the reef facies in Perryfield and Coombefield quarries. During 1990–1992, Coombefield was expanding very rapidly and at least 20 reefs were examined. These localities are marked on Text-figure 1. As mentioned above, the reef facies seems to be more widely developed in the southern part of the island. Reefs are unknown in the Portlandian rocks of the mainland.

STUDY METHODS

We have studied *in situ* reefs and quarried blocks derived from them. Data on shape, composition, orientation, and lateral passage into flanking sediments have been obtained in the field, and an extensive fauna has been collected. Large, orientated slabs have been cut and polished on a vibrating lap, yielding a wealth of information about compositions and textures that cannot be seen on unpolished material. Data on proportions of different reef components and biovolumes of the main framebuilders have been obtained from these surfaces by overlaying them with a 5 mm grid marked on a transparent overlay and point counting at the intersections. Amounts of material removed from the reef by small borers were obtained by point counting on acetate peels of polished surfaces viewed through a petrological microscope. Bulk samples of the reef were broken up, sieved, and picked until several examples of even the rarest elements of the fauna had been collected or observed.

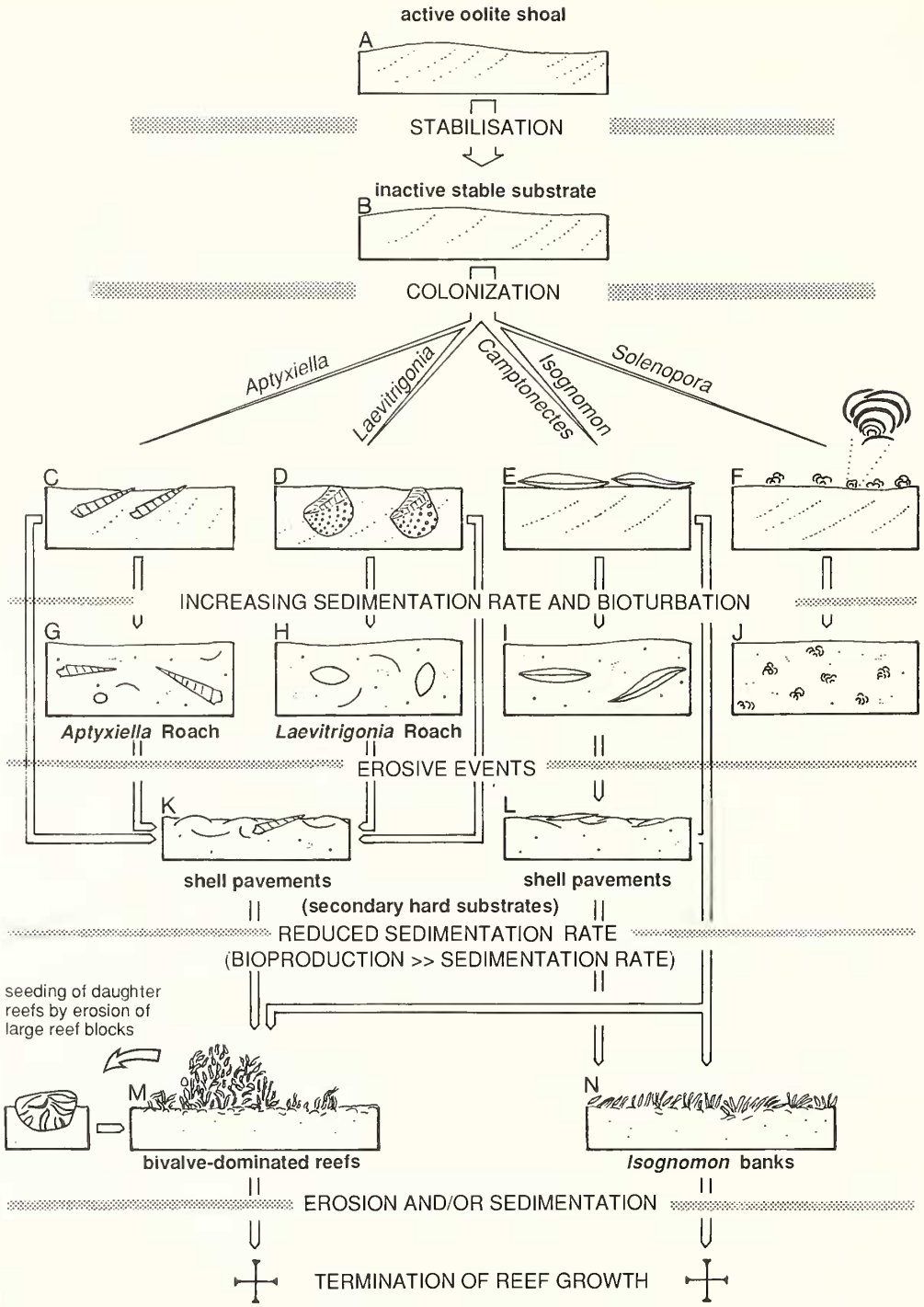
Repository. Collections are housed in the Oxford University Museum.

ENVIRONMENTAL FRAMEWORK

Colonization of the Upper Portlandian sea-floor

The abundant benthic fauna in the Roach Bed suggests that the oolith shoals of the Portland Freestone Member did not remain actively growing right up until the onset of Purbeck deposition, but passed into a stable phase when colonization occurred. The heavily-micritized state of the ooliths supports the idea of a prolonged period of stable bottom conditions after the main episode of shoal growth, and the diversity of both infauna and epifauna would not have grown on constantly shifting, unstable, active oolith shoals.

The normal fauna of the Roach is dominated by soft-sediment dwelling bivalves (particularly *Laevitrigonia*) and gastropods (*Aptyxiella*), which may occur together or in assemblages dominated by one or the other. Locally, small (*c.* 10 mm across) *Solenopora*, encrusting small shell fragments, are prevalent. A fourth variation contains conspicuous *Camptonectes* and *Isognomon* (Text-fig. 2). Many of the bivalves are found articulated and there is little sign of current sorting or abrasion, though locally there are signs of current orientation of single valves. However, both gastropod and bivalve shells, including those of the burrowing species, are encrusted by an epifauna of bryozoans and oysters, which often attach to the inner faces of the valves. This suggests that dead shells lay on the sea floor for some time before eventual burial. Locally, these shelly layers supported *Camptonectes* and, particularly, *Isognomon* in great profusion. Again, they are usually articulated, yet are encrusted inside and out. In life, they must have formed extensive banks. These observations indicate that conditions on the sea-floor were not subject to any great current activity (though probably intermittent storms caused local shell orientation), and were conducive to growth of abundant life. We agree with Townson's (1975) view of a fully marine environment in shallow water on top of a prograding carbonate platform, in which organic growth was the principal sedimentary process. Thus, once the formerly active oolith shoals had stopped shifting around, skeletal growth became the dominant sedimentary process and their history was one of colonization by a benthos, with gradual accumulation of shells and occasional episodes of winnowing leading to a change in

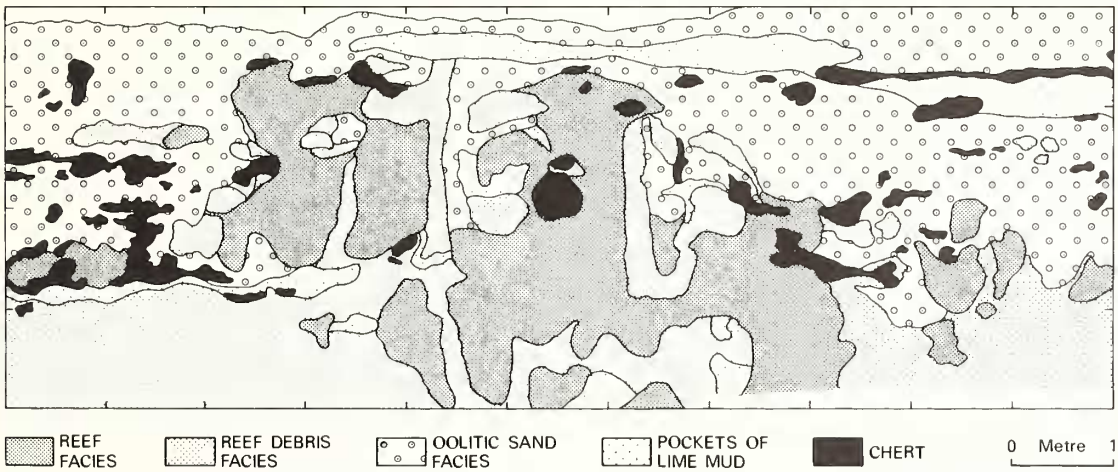


TEXT-FIG. 2. Generation of shell pavements on which Portland patch-reefs initiated and grew, as a result of episodic winnowing of the fauna of the inactive shoals of oolitic lime sand.

the character of the sea-floor. This taphonomic feedback (Kidwell and Jablonski 1983) resulted in gradual replacement of a soft-sediment infaunal benthos by a shell-pavement epibenthos. Events are summarized in Text-figure 2.

Reef growth and composition

It was against this sedimentary background that, locally, successive generations of encrustation by a variety of frame-building organisms started to build up biocemented frameworks which, in turn, attracted further encrustation and developed into small reefs. The smallest such buildups are only a few tens of centimetres across, but locally the process went on for a long time, eventually resulting in bioherms as large as 7 m across and 3·5 m high. A section through the largest reef body exposed during the course of this study is shown in Text-figure 3. It is difficult to get a clear picture of the



TEXT-FIG. 3. Facies distribution in a vertical section taken through a large patch-reef in the north-east corner of Suckthumb Quarry (see Text-fig. 1).

three-dimensional shapes of many of the reefs because of the two-dimensional exposure and the rubble surrounding them in the working quarry faces. The strength of the reef fabric initially came from the principal framebuilders, but the porosity within the frame acted as a site for the precipitation of large volumes of peloidal calcite marine cement, which rapidly converted the primary organic structure into a dense reef-rock (Pl. 1, figs 1–2; Pl. 2, figs 1–2). This peloidal fabric is often laminated, due to variations in peloid size from layer to layer (Pl. 2, figs 1–2), and fills some of the primary cavities geopetally. It is structurally identical to early marine cements that have been described from a variety of reefal settings from ancient (see references in Sun and Wright 1989, and Mock and Palmer 1991) and Recent (Macintyre 1985) settings, and for which some workers have proposed a bacterially-mediated origin (Chafetz 1986).

The peloidal cement fills smaller spaces between the main framebuilders, and is particularly abundant in borings that perforate the primary fabric, and inside articulated shells (Pl. 2, fig. 2). Larger intrareefal cavities locally contain detrital sediment, such as ooliths and unpelleted lime mud which is burrowed (Text-fig. 3). Relative proportions of the different components differ within the reef body, and around the edges of reef blocks where active reef growth had ceased and where bioerosional processes dominated (Pl. 2, fig. 3). In this distinct edge sub-facies, many generations of boring, precipitation of peloidal cement in the borings, and reboring alternated. As a result the edge facies has a significantly higher proportion of marine pelleted cement than is found deeper into the reef. These differences in the percentage volume contributions of the different organic and

inorganic constituents of the reefs, which were obtained by point counting as discussed above, are summarized in Text-figure 4.

Relationship of reefs to adjacent soft sediment

Oolitic sediments abut against the sides of the larger reef bodies and locally fill voids within the reef structure (Text-fig. 3). Smaller reefs are covered by such sediment, which must have accumulated at a rate greater than reef growth, or else have washed over them during occasional high energy events. The largest reefs intersect the top of the Portland and are directly overlain by Purbeck sediments.

There is plenty of evidence for erosive processes carrying material off the reefs into the adjacent oolitic sands. Immediately next to the reefs, many large shells of reef-dwelling and frame-constructing species are found in the oolitic matrix (Text-fig. 5). Further away from the reef, abundances of reefal groups and the sizes of the derived fragments decrease, so that more than about 20 m away there is no indication of the proximity of the reef, and the normal soft-sediment Roach assemblages are seen. We have not been able to see whether this detrital apron extends farther in one lateral direction than any other, which might suggest a windward and a seaward direction. Small blocks of the primary frame, apparently broken off larger reefs and lying close to them, provided sites for further encrustation and growth (Text-fig. 3). Sometimes these daughter reefs subsequently coalesced with the parents that spawned them.

LATER DIAGENESIS

All facies of the Portland Roach are characterized by complete leaching of aragonite, so that all aragonitic taxa are preserved as internal and external moulds (Pl. 2, fig. 1). The dissolution probably occurred very soon after completion of sedimentation when the sequence was uplifted into the meteoric realm. The overlying basal Purbeck rocks contain soils and freshwater ostracodes (Arkell 1947; Townson 1975; R. C. Whatley pers. comm.) so downward flow of meteoric water through at least the upper part of the Portlandian sediments must have occurred, and would probably have been rapid at some times during the year, given the marked seasonality of Lower Purbeck times (Francis 1984). In contrast to the fate of aragonite, low-magnesian calcite shells of bryozoans, brachiopods, some molluscs, and the winter layers (cf. Wright 1985) of the rhodophyte *Solenopora* are preserved with full microstructural detail, and show only some mild silicification (presumably the result of remobilization of silica from sponge spicules; Townson 1975). However, a third style of preservation is evident in serpulids, encrusting forams (*Nubeculinella*), and in the darker summer layers of *Solenopora*. In these taxa preservation is variable, ranging from good (with little or no apparent structural alteration) to mouldic (with complete loss of original shell; Pl. 1, fig. 2). In between (particularly in *Solenopora*) lie examples of partial replacement by diagenetic calcite with varying amounts of loss of detail of the original microfabric. This style of replacement has been noted in *Solenopora* of Middle Jurassic age by Wright (1985) who favoured the explanation that composition fluctuated between low- and high-magnesian calcite (LMC and HMC) across the seasons and that the latter was replaced by aragonite early in diagenesis. Given that the degree of dissolution is never as clear-cut as in the unequivocally aragonitic shells, we support an original

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EXPLANATION OF PLATE 1

Figs 1–2. Two pieces of Portland patch reef showing three of the four principal framebuilders: *Solenopora* (S), *Plicatula* (P), and *Liostrea* (L), surrounded by sedimentary matrix which is either precipitated micrite peloidal cement (C) or oolitic grainstone that has been washed into the reef from the surrounding oolite shoals (O). Large borings (B) containing articulated *Lithophaga* cut across both the skeletal frame and the synsedimentary cement. Polished blocks. Large squares on scale grids are 10 mm.

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HMC composition for *Solenopora* and the other variably-preserved skeletons, with magnesium levels possibly varying throughout the year in response to temperature or growth rate. Styles of dissolution of HMC depend on a range of factors such as microstructural detail, the original magnesium levels in the calcite, the concentrations of dissolved carbonate in the diagenetic fluids, and the evolution of the pore-water chemistry with increasing burial (Walter 1985). Variations in these probably led to the differences in the degree of alteration of putatively HMC skeletons that are now preserved, and we see no reason to support an additional diagenetic episode involving differential replacement of HMC by aragonite.

It is not so much the loss of aragonite that makes the Roach remarkable, but the fact that the moulds were not filled by later diagenetic calcite cement. There is a small amount of this cement, mostly growing as a thin sugary veneer on some of the aragonite moulds and in the small pore spaces inside borings or between the peloids of the early marine cements, but it is volumetrically a minor component. It may be that, the aragonite and some of the HMC having been flushed out of the system during meteoric emergence at the end of Portland times, there was no major source of dissolved carbonate when the sequence eventually became buried. Indeed, the whole Portland sequence may have been diagenetically closed, sandwiched between the underlying Kimmeridge Clay and the overlying clay-rich Purbeck and Wealden.

REEF ECOLOGY: GROWTH, COLONIZATION AND BIOEROSION

Ecological guilds

We have recognized five ecological guilds into which all of the fauna of the Portland reefs can be placed. These provide a convenient structure for a discussion of the dynamics of reef growth and destruction. These guilds are: (1) the principal organic framebuilders; (2) the accessory framebuilders of small cementing encrusters; (3) the interstitial fauna of nestlers and predominantly soft-boiled sessile forms; (4) vagile strollers on the reef surface; and (5) the borers that excavated dwelling holes in the skeletons of the primary framebuilders and in the cemented reef rock. A summary of the complete reef and reef-associated fauna, together with the guild assignations, is given in Table 1.

Principal framebuilders

There are four major taxa that are responsible for the biogenic frame of the reefs. Most conspicuous is the red alga *Solenopora 'portlandica'* (Pl. 1, figs 1–2), which ranges in size from small knobs only about 10 mm across to large cauliflower-shaped heads as much as 0·3 m high. (This species has yet to be formerly described, although it is widely known in the literature (e.g. Wright 1985) under this name.) Growth banding is very conspicuous and the largest specimens display as many as fifty alternations of lighter (winter) and darker (summer) layers. However, although *Solenopora* is locally very common and conspicuous in some of the reefs, elsewhere it may be rare or absent altogether.

The framebuilders that are most widespread, and which make the biggest contribution in terms of volume to all the reefs examined, are bivalves. The first is *Liostrea expansa* J. Sowerby (Text-fig. 5), a thick-shelled oyster that grows in a somewhat cup-shaped form (probably as a result of crowding). The range of shape and size variation is difficult to assess because the shells cannot easily

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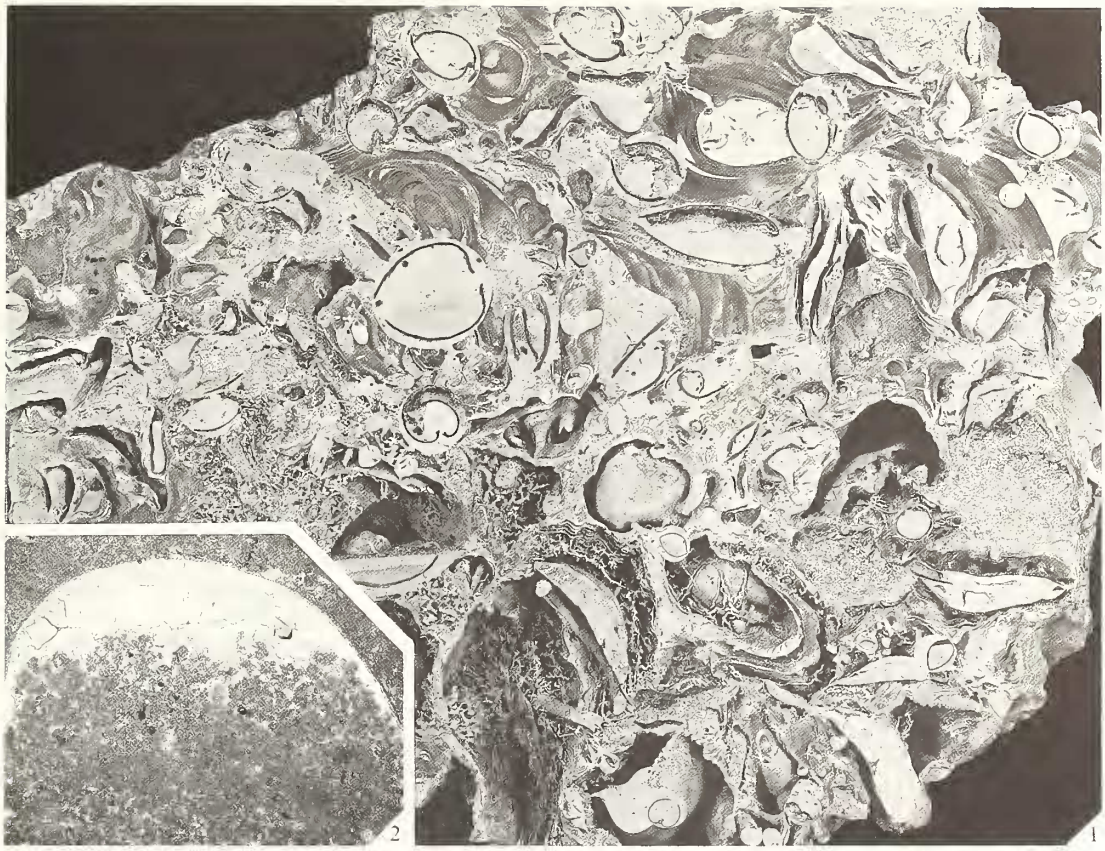
EXPLANATION OF PLATE 2

Figs 1–2. Structure of reef rock from the Portland reefs. 1, polished slab showing primary biogenic fabric of oysters (dark laminated shells) and *Plicatula* (with biomouldic preservation) surrounded by peloidal micrite cement. Both are cut by bivalve borings, which are in turn filled with later generations of laminated peloidal cement; ×0·8. 2, acetate peel of laminated geopetal peloidal early marine cement inside bivalve boring; ×18.
Fig. 3. Large *Lithophaga* boring into edge of patch reef; ×0·6.



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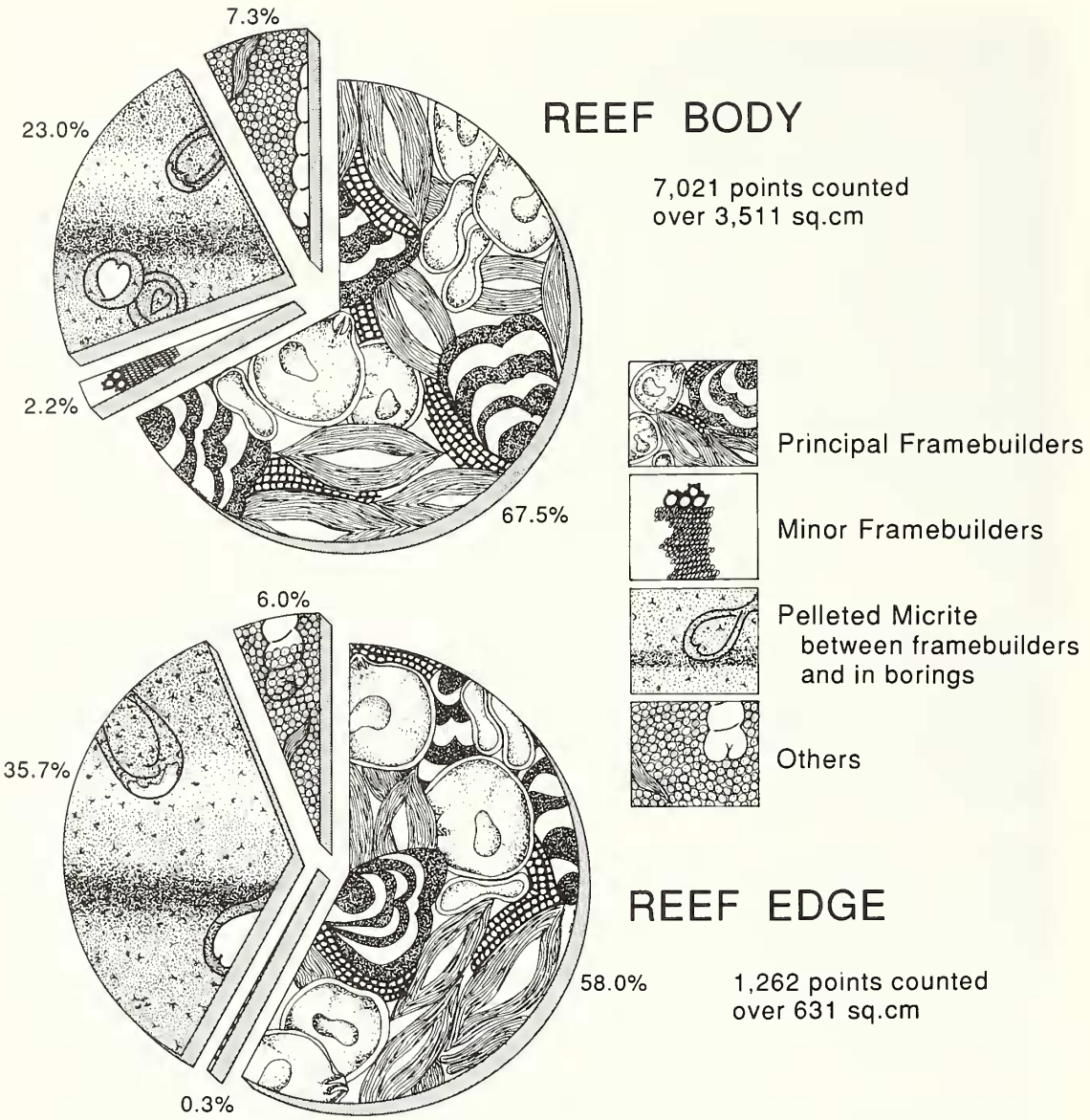
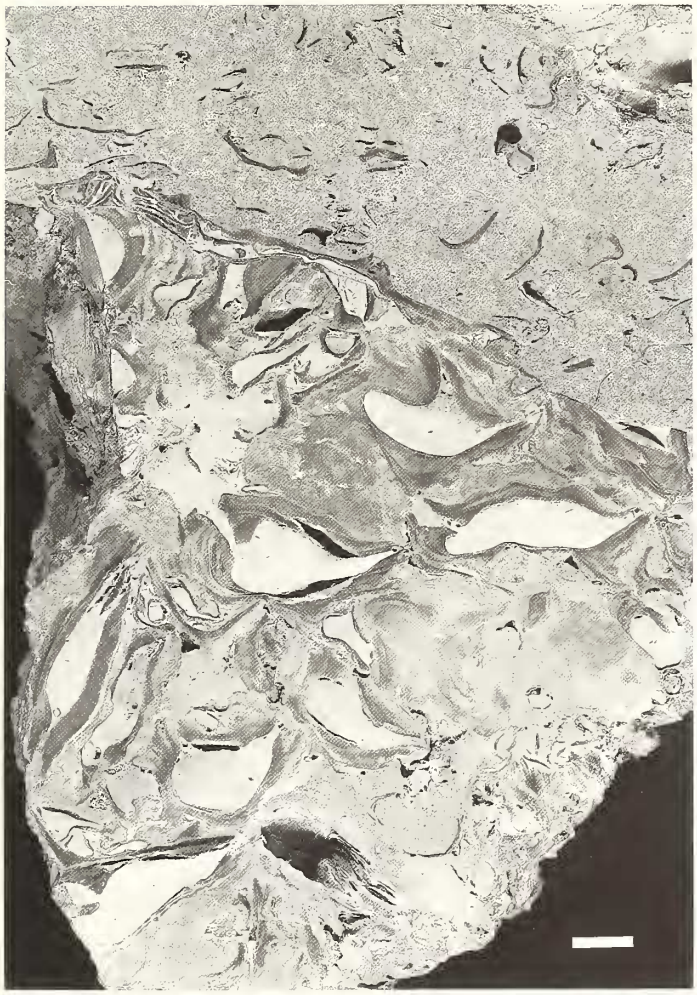


TEXT-FIG. 4. Different proportions of components in the main reef body and at the edges of mature reefs. The greater amount of peloidal cement in the latter is mostly located within borings, which occupy a larger proportion of the overall volume at the reef edge.

be extracted whole from the reef. The second bivalve is *Plicatula damoni* Cox (Pl. 2, fig. 1) which is easy to study because the valves were composed of a thick (*c.* 5–6 mm) inner aragonite layer and a thin exterior layer of calcite folia. The former has dissolved during diagenesis, freeing the internal moulds which are largely composed of peloidal cement. Because of crowding and overgrowth, they are very variable in shape and size, and attain a maximum height of 50 mm.

The fourth principal framebuilder, which is only present in some of the reefs, is the massive multilamellar cyclostome bryozoan *Hyporosopora portlandica* (Gregory). Uniquely among Jurassic



TEXT-FIG. 5. Junction between reef and overlying oolitic sediment containing skeletal debris that was washed off the reef. In this sample, the reef is largely composed of massive bryozoans (*Hyporosopora portlandica*) with embedded oysters. Scale-bar represents 10 mm.

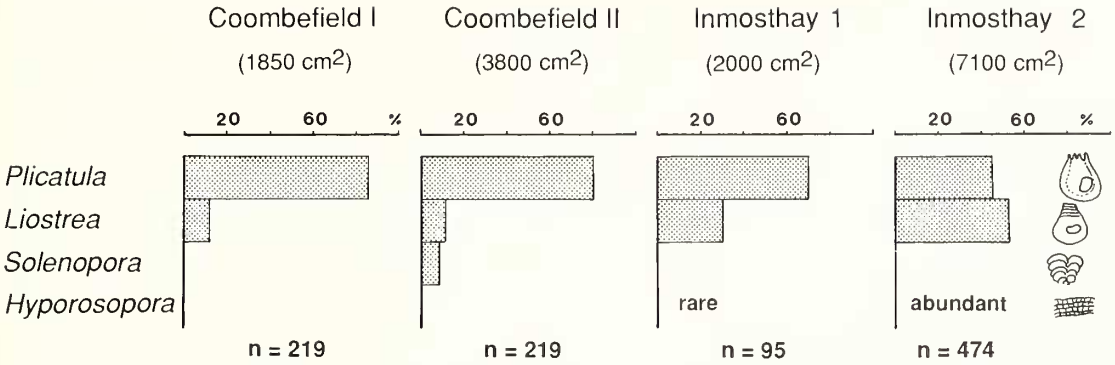
Bryozoa, what are apparently single colonies can reach as much as a metre across and several tens of centimetres thick. Polished vertical sections show lighter and darker zones of about five zooecial layers in thickness, which reflect differences in zooecial size that may be seasonal. Bivalved oysters are widely embedded in these massive bryozoan colonies (Text-fig. 5).

We have studied the relative contributions of the four main framebuilders to the buildups in two ways. In the field, we counted numbers of individuals of the four types on known areas of vertical sections through four different reefs at two localities (Text-fig. 6). The results show some of the variation, particularly in the abundance of *Solenopora* and *Hyporosopora*, but numbers alone do not give a clear indication of the contribution of each species to reef growth. We thus studied biovolume by point-counting cut and polished surfaces of twenty three blocks collected from several different reefs in Coombefield Quarry, subjectively distinguishing between the reef body and the reef edge sub-facies. The total area examined in this way was over 0·64 m^2. The blocks were chosen for appropriate size rather than by composition, so the proportions of the different framebuilders are likely to reflect actual proportions in the reefs thus sampled. However, some of the blocks were lying loose in the quarry, so it is not possible to say how many reefs are represented. Results of this exercise are shown in Text-figure 7, and clearly show that reef growth is dominated by the bivalves.

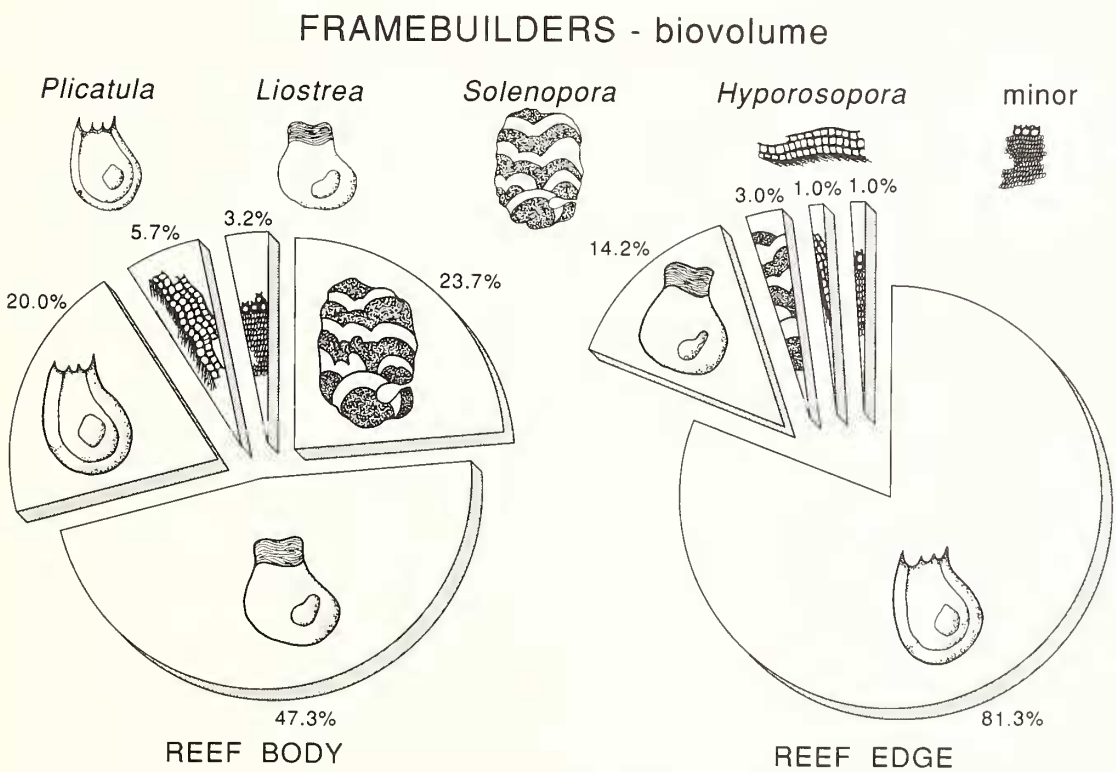
TABLE 1. Summary of species in the five reef guilds of the uppermost Portlandian, Isle of Portland, Dorset. Key: +, trace fossil; ++, bioimmuration; ×, new record or first assignation of this taxon to the British Portlandian; (×), species previously recorded, but new material gives more detailed morphological information.

Principal framebuilders	
Algae	
Solenopora 'portlandica'	
Bivalvia	
Plicatula dannoni Cox	
Liostrea expansa (J. Sowerby)	
Bryozoa	
Hyporosopora portlandica (Gregory)	
Accessory framebuilders	
Stomatopora sp.	
Nubeculinella sp.	×
Porifera	
lithisthid indet.	×
'Worms'	
Serpula (*Cycloserpula*) *gordialis* (v. Schlotheim)	
Serpula (*Cycloserpula*) *striatissima* sp. nov.	×
Serpula (*Dorsoserpula*) *sp.*	
+ agglutinating worm tube	×
Bryozoa	
'Berenicea' sp.	
Stomatopora sp.	
Interstitial fauna	
Porifera	
Rhaxella sp.	
Pachastrella sp.	
Bivalvia	
Barbatia (*Barbatia*) *bourgueti* de Loriol	×
Cucullaea (*Idonearca*) sp.	
Modiolus (*Modiolus*) sp.	
Isognomon bouchardi (Oppel)	
Plagiostoma sp.	
Hiatella (*Pseudosaxicava*) *phaseolus* (Eudes-Deslongchamps)	(×)
Bryozoa	
++ *Stolonicella* sp.	×
Brachiopoda	
micromorphic terebratulid indet.	×
Incertae sedis	
++ bioimmured 'dimples'	×
Strollers	
Bivalvia	
'Lucina' portlandica J. de C. Sowerby	
Gastropoda	
Uchauxia quadrigranosa Cox	
naticid indet.	
medium-spired gastropod indet.	
pleurotomariid indet.	
Annelida	
+ *Arachnostega gastrochaenae* Bertling	×
Borers	
Thallophytes	
+ unidentified filaments	×
Porifera	
+ *Entobia cervicornis* isp. nov.	×
'Worms'	
+ *Caulostrepsis cretacea* Voigt	×
+ *Spirichnus spiralis* igen. et isp. nov.	×
+ *Cunctichnus probans* igen. et isp. nov.	×
Bivalvia	
Lithophaga (*Lithophaga*) *subcyclindrica* (Buvignier)	×
Lithophaga sp. A	×
[+ *Gastrochaenolites torpedo* Kelly and Bromley]	×
Carterochaena pulcherrima gen. et sp. nov.	×
Gastrochaenopsis recondita (Phillips)	×
[+ *Gastrochaenolites dijugus* Kelly and Bromley]	×
Phoronida	
+ *Talpina bronleyi* isp. nov.	×
Bryozoa	
+ *Iramena* isp.	×
Crustacea	
+ *Rogerella pattei* (Saint-Seine)	×

The dominance of *Plicatula* in the reef-edge sub-facies reflects the density of borings there. *Plicatula* can grow in highly twisted and distorted shapes and sometimes occupies vacated bivalve borings, or perches on pinnacles between borings. This flexibility of growth form would have made it an effective competitor for the limited space in the growing reef. The other framebuilders seem less able to cope with the vicissitudes of this highly competitive and bioerosive environment. Moreover, the

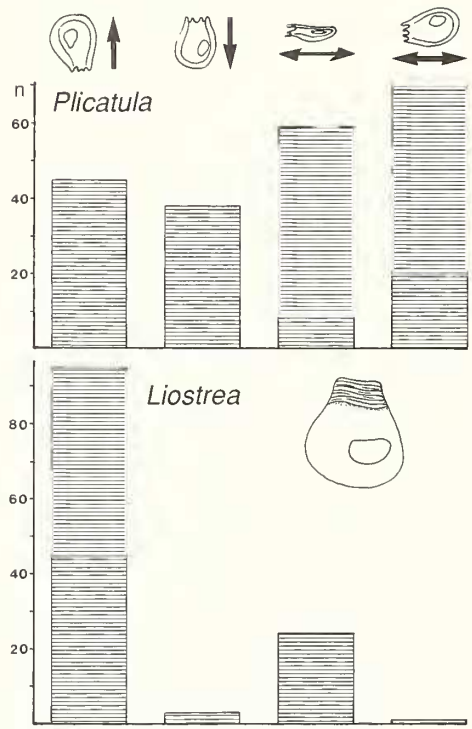


TEXT-FIG. 6. Proportions of the four principal framebuilders (by number) in two reefs from Coombefield and two from Inmosthay Quarries.



TEXT-FIG. 7. Relative proportions (by volume) of the four principal framebuilders in the main reef body and at the reef edge. Data obtained by point counting on polished blocks; see text and Text-figure 6 for details.

bivalves are likely to have been faster growing than the more massive framebuilders, less controlled by incident light than *Solenopora*, and able to produce large numbers of individuals, which often settled and grew in bundles, in frequent recruitment episodes to take advantage of new attachment areas as soon as they became available.



TEXT-FIG. 8. Orientations of *in situ Liostrea* and *Plicatula*, taken from field observations of reefs in Coombefield and Inmosthay Quarries.

Liostrea and *Plicatula* also exhibit different orientation patterns and hence growth strategies (Text-fig. 8). Individuals of *L. expansa* grew preferentially upward, whereas *P. damoni* seems to have been able to grow in any orientation. In terms of numbers of individuals, *Plicatula* is usually the most abundant framebuilder and was able to occupy the sides of the reefs and overhangs from which it grew outwards and downwards, as well as growing upwards from the reeftops. It was thus a major contributor to reef lateral expansion as well as upward growth. In contrast, the preference for the oysters to grow with negative geotaxis suggests that their main contribution to reef growth was in the upward direction.

Accessory framebuilders

The accessory framebuilders are dominated by small lamellate bryozoans, serpulids, and encrusting forams. Runner-type bryozoans (*Stomatopora*), small oysters (including both *Nanogyra* and other

EXPLANATION OF PLATE 3

Figs 1–2, 4. *Arachnostega gastrochaenae* Bertling. 1–2, OUM J53650; latex cast of negative reliefs on the surface of an internal mould of *Plicatula*; 1, ×3; 2, ×15. 4, OUM J53652; calcite-filled endorelief at the surface of internal mould of *Plicatula damoni* Cox; ×2.

Fig. 3. *Serpula* (*Cycloserpula*) *striatissima* sp. nov. OUM J53653, holotype; latex cast of external mould; ×10.

Fig. 5. Dimpled structures, latex cast, preserved by bioimmuration on internal mould of *Plicatula*, OUM J53654; ×12.

Fig. 6. Bundled scratch marks, preserved as positive relief near the adductor muscle scar of *Plicatula*, OUM J53655; ×12.

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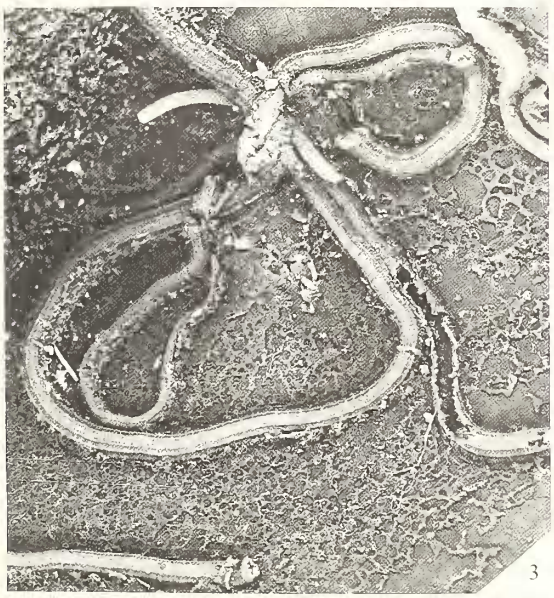
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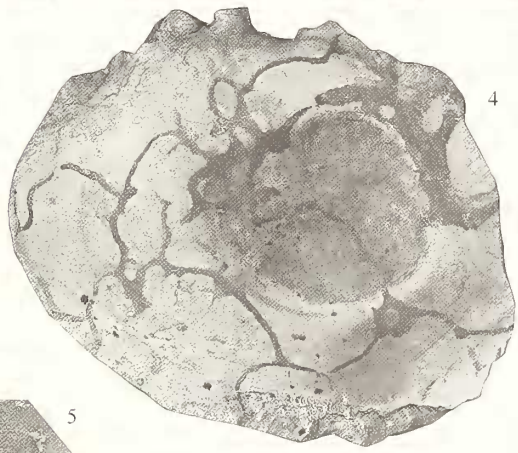
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FÜRSICH *et al.*, Portland reef biota

forms which may be small *L. expansa*; it is difficult to distinguish between them in cross-section) and agglutinated tubes occur more rarely. Also occurring rarely, but as quite large individuals, is an unidentified lithistid sponge, the first recorded from the Portlandian of England. The accessory framebuilders as a whole are difficult to study as they are firmly embedded in the reef matrix and cannot be extracted. The larger ones, however, can be recognized in cross-section and have been included as a separate category in the point-counts (Text-figs 4 and 7).

There is one microenvironment in the reef where relative abundances of the different small encrusters can easily be studied. This is inside articulated *Plicatula*. Here, the encrusters grew inside at least 60 per cent of the dead shells and were subsequently smothered by sediment or marine pelleted cement. Subsequent dissolution of the aragonite shell leaves this sedimentary filling as a well-preserved steinkern (Pl. 3, figs 1 and 4) that shows the attachment faces of the encrusters that are embedded in it and which were originally attached to the inner faces of the valves. Alternatively, encrusters that have themselves dissolved away leave external mouldic impressions in the steinkern surface (Pl. 3, fig. 3). Text-figure 9 shows relative numbers of *Plicatula* in three different reefs that have encrusters of different species in them. Although this small cryptic microenvironment might be expected to have a somewhat specialized encrusting fauna, we anticipate that much of the surface space in the reefs that was available to accessory framebuilders would have been of a cryptic kind, in limited spaces down between the main framebuilders and in the reef interior. Typical Jurassic upward-facing, open-surface encrusters such as *Nanogyra* and large *Dorsoserpula* occur rather rarely in the reef body.

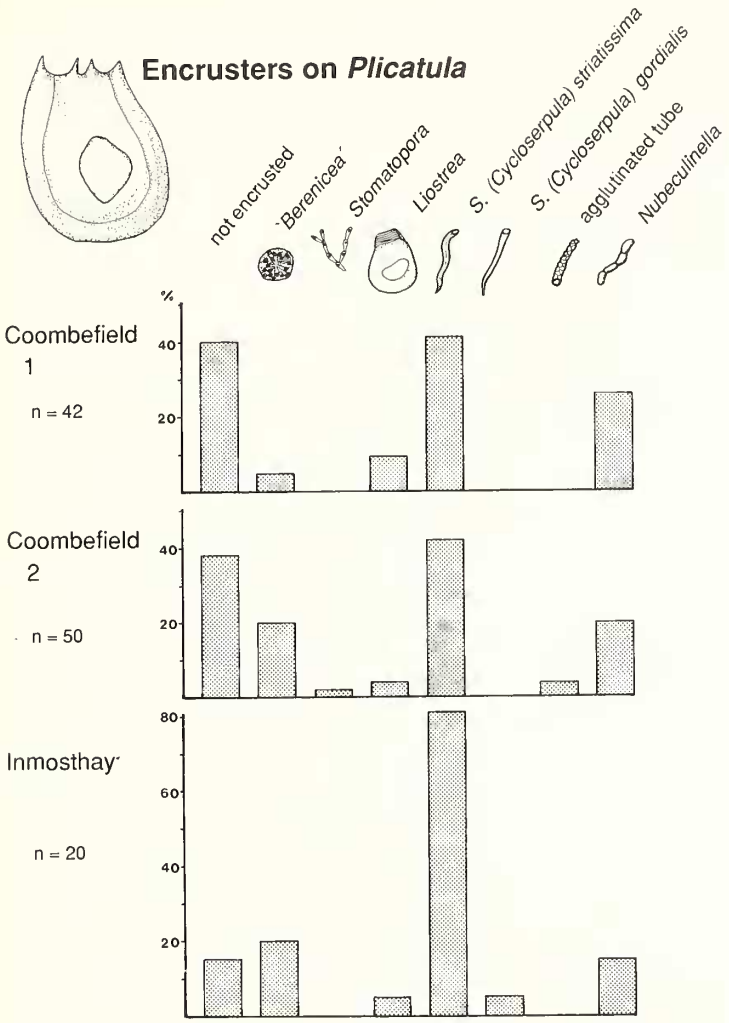
Interstitial fauna

The most conspicuous members of the interstitial fauna are the byssate bivalves that nestled inside bivalved shells, old borings, and other small cavities. These include the familiar arcids and mytilids widely seen in Jurassic rocks, but there are also large numbers of *Hiatella* which is generally poorly known from the Jurassic, probably because the small, thin-shelled individuals are likely to be overlooked in facies that do not show mouldic preservation. The great majority of the *Hiatella* in the Portland reefs are found nestling inside the vacated crypts of boring bivalves, sometimes inside the gaping shells of the borers that made the holes in the first place. Indeed more than one pair of *Hiatella* valves can be found, later occupants inside earlier ones. They are very variable in shape and size (though never more than 10 mm long) and clearly modified their shape to fit the hole they nestled in. There is no indication that they enlarged or modified this hole in any way; they merely squatted, as did the Lower Cretaceous *Hiatella* described by Kelly (1980).

We also regard the worms that lived inside the sedimentary fills of dead shells and vacated borings as part of the interstitial fauna. The burrows that they made are most clearly seen as grooves in the surfaces of *Plicatula* and *Lithophaga* steinkerns, where their burrowing activity was deflected along the inside face of the shell (Pl. 3, figs 1–2, 4). These net-like burrow systems are extremely widespread in fossil internal moulds generally (particularly in Mesozoic rocks, but we have seen examples from the Ordovician), and have recently been described under the name *Arachnostega* by Bertling (1992). They are discussed more fully in the systematic section below.

A major contribution to the living reef appears also to have been made by demosponges that are now only represented by calcite casts of their originally opaline silica spicules. Thin sections through interstitial sediment and patches of pelleted cement show an extraordinary abundance of the tiny bean-shaped microscleres (selenasters) of *Rhaxella*, together with lesser numbers of the tetraxon megascleres of *Pachastrella*. *Rhaxella* is closely related to the Recent *Placospongia* (Hinde 1887–1912) which is common in Recent coral reefs in the western Atlantic (Rützler 1978; Rützler and Macintyre 1978).

There are two additional minor curiosities among the interstitial fauna. The first is the first record from the Portland Limestone of terebratulids, albeit very rare and very small. The second is the preservation by bioimmuration (see Taylor 1990) of minute dimpled structures, consisting of hemispherical mounds *c.* 0·25 mm across, with a little hole in the top (Pl. 3, fig. 5). In some, this hole



TEXT-FIG. 9. Patterns of encrustation of inner faces of articulated *Plicatula* by the most common of the accessory framebuilders in two reefs from Coombefield and one from Inmosthay.

appears to have been enlarged, as if by emergence of an inhabitant. We suspect that they are eggs of an unknown invertebrate.

Vagile fauna

'Strollers' are limited to gastropods, of which the tiny procerithiid *Uchauxia quadrigranosa* Cox, which we envisage as a grazer and scavenger with catholic dietary tastes, was by far the most common. The absence of echinoids, which are such a prominent member of this guild in Recent reefs and in other Jurassic reefal settings (e.g. Fürsich 1977; Palmer and Fürsich 1981), remains something of a mystery.

Borers

The feature of the Portland reefs that first drew our attention to them was the variety and abundance of the borings. They occur both in the overall reef-rock framework and in individual shells. They are easiest to study where they entered *Plicatula* valves, and later became filled by

precipitation of the early pelleted cement. Exquisite natural cement casts have been revealed by the subsequent aragonite dissolution.

The largest and most conspicuous borings are examples of *Gastrochaenolites torpedo* Kelly and Bromley that may reach 60 to 70 mm in length. They were made by *Lithophaga subcylindrica* Buvignier, and are most common in the cemented reef-rock, particularly in the reef edge facies where active expansion of the reef had stopped and bioerosive processes became predominant (Pl. 2, fig. 3). Locally, they cross empty cavities such as the spaces inside articulated shells, so it seems the boring bivalve was not put off by breaking through into a void, but continued through to the wall on the far side. This behaviour was not shown by either of the other boring bivalves, which are both gastrochaenids.

Even more numerous than *Lithophaga* crypts are borings of the bivalves *Carterochaena* and *Gastrochaenopsis* which differ from those of *Lithophaga* by being smaller, and having a circular cross-section in the lower half but a figure-of-eight cross-section in the upper part. This is the result of a secreted lining to the mouth of the boring, isolating the shell inside, except for the holes for the siphons to pass through. Many Recent gastrochaenids show such a structure, made of aragonite and secreted by the siphonal walls (Carter 1978). However, the lining is preserved in our material (in the borings of both species), and does not show the mouldic preservation of aragonite. We think that it was either secreted calcite, or made of a paste of very fine calcite particles released in boring.

The borings themselves can be accommodated in the ichnospecies *Gastrochaenolites dijugus* Kelly and Bromley. Those of *Carterochaena* reach a length of about 12 mm and appear limited to the primary framebuilders, particularly the valves of the bivalves. *Gastrochaenopsis* reaches nearly 20 mm and is particularly common in the cement-rich reef edge sub-facies, alongside *Lithophaga*.

Apart from the fairly large bivalve borings, there occur a number of smaller, more delicate borings which have been created by members of several phyla ranging from sponges (*Entobia*), phoronids (*Talpina*), crustaceans (*Rogerella*) to bryozoans (*Iramena*) and various kinds of 'worms' (*Caulostrepsis*, *Cunctichnus*, and *Spirichnus*). Despite their small size (most of these borings have a diameter of 1 mm of less), they are very conspicuous, because they either form extensive three-dimensional ramifying systems (*Entobia*) or else occur in high density (e.g. bundles of *Talpina* and *Spirichnus*). They are very conspicuous and occur profusely with exquisite preservation as natural casts in the voids after dissolution of the aragonite of the *Plicatula* valves (Pl. 4, fig. 1). They also occur with similar densities in the oysters, and the rigidity and mechanical strength of many of the bivalve framebuilders must have been severely weakened.

Counts of borings in more than two hundred *Plicatula* shells from four different reefs showed that between 60 and 100 per cent of the shells contained at least some borings (Text-fig. 10). *Gastrochaenolites* and *Entobia* were most abundant, followed by *Spirichnus*, *Talpina*, *Cunctichnus*, and *Caulostrepsis*. Of least importance were the acrothoracican barnacle boring *Rogerella* and ctenostome bryozoan borings. In order to get an estimate of the relative importance of the various borers as destroyers of the reef framework, which cannot be judged from their relative numbers alone, point counts were made on acetate peels from the reef edge where bioerosion was noted to be most extensive. As Text-figure 11 shows, more than 40 per cent of the framework has been destroyed by boring organisms, with *Gastrochaenolites* being about twice as important as the rest. Boring bivalves are particularly common at the reef edge; towards the reef core the volume of reef structure destroyed by borers appears somewhat smaller. We suspect that the amount of material

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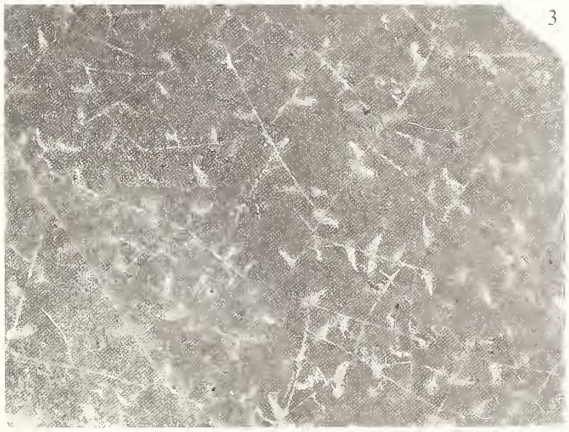
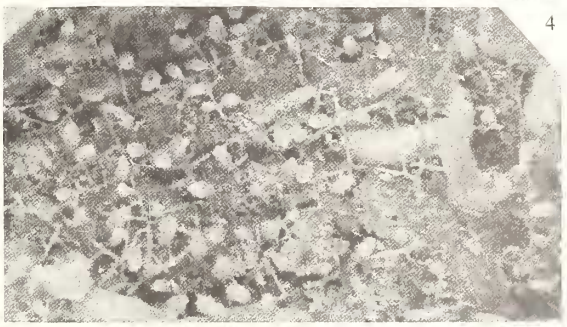
EXPLANATION OF PLATE 4

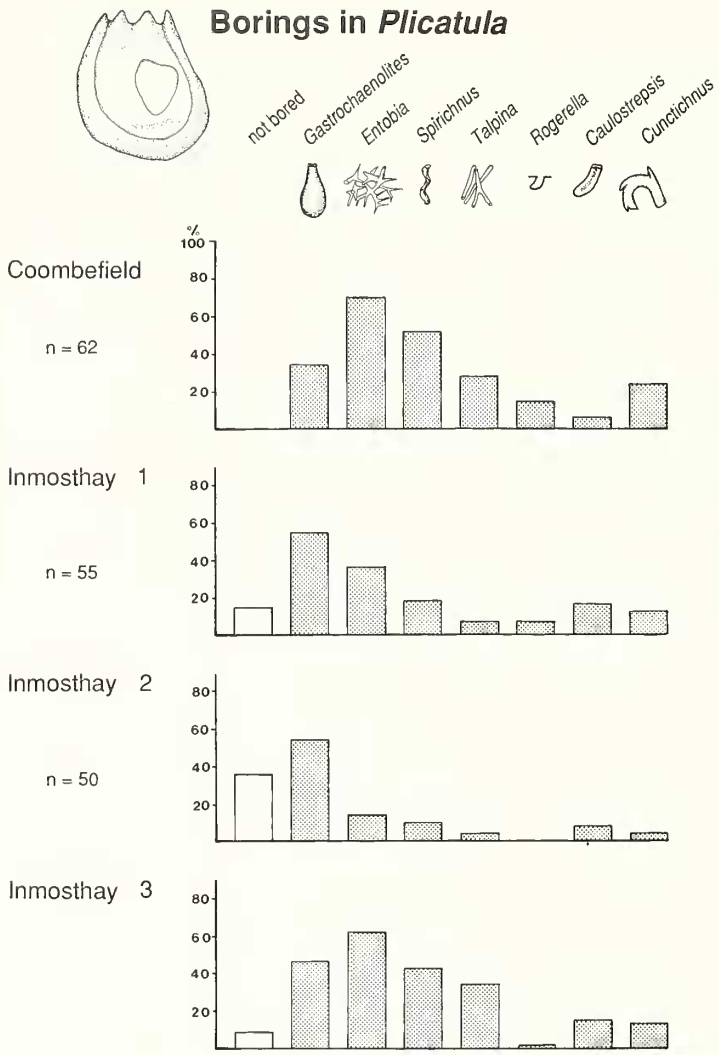
Fig. 1. Natural casts of small borings in the aragonite inner shell layer (now dissolved) of *Plicatula*, including *Talpina* (left centre), *Spirichnus* (centre and upper right), and *Entobia* (lower centre), OUM J53680; ×6.

Figs 2–4. *Iramena* ichnosp., boring of ctenostome bryozoan. 2–3, surface view of boring network in oyster shell; 2, OUM J53681; ×10; 3, OUM J53682; ×16. 4, natural cast in aragonite shell layer (now dissolved) of *Plicatula*, OUM J53683; ×15.





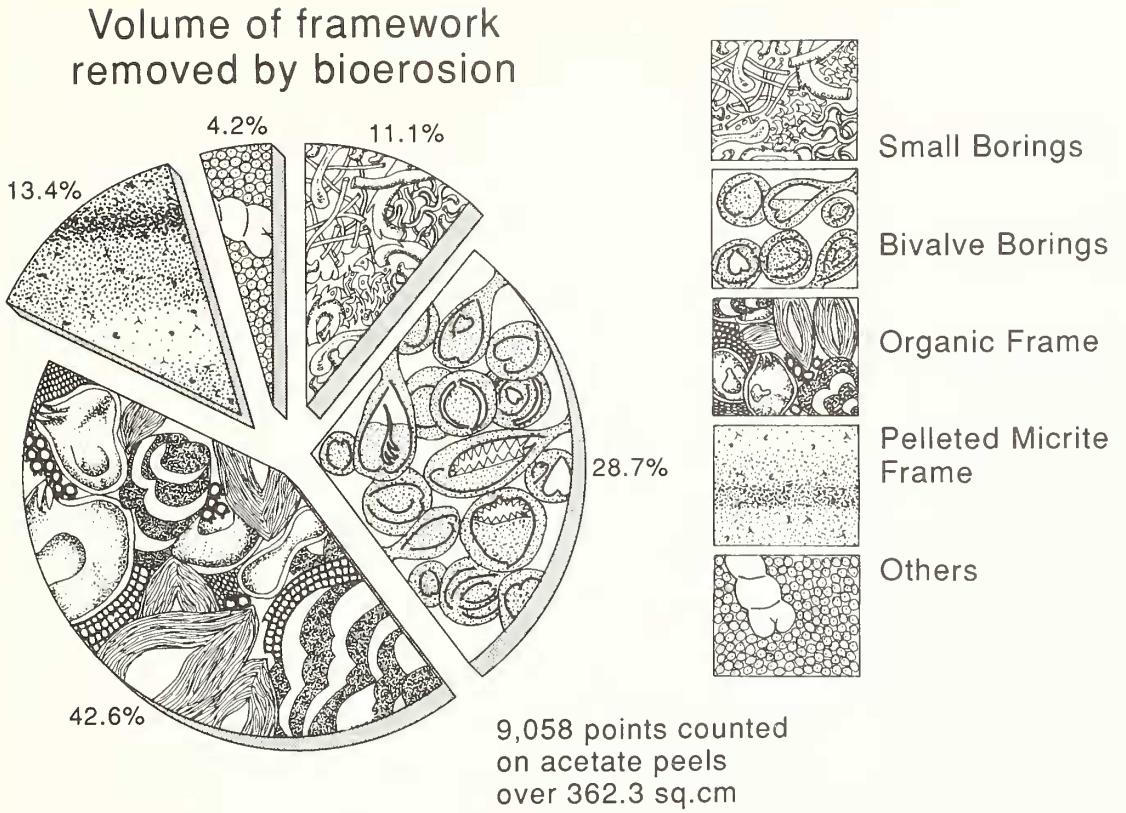
FÜRSICH *et al.*, Portland reef borings



TEXT-FIG. 10. Distribution of borings in *Plicatula* (percentage of individuals containing different borings) based on field observations on three reefs in Inmosthay Quarry and one in Coombefield Quarry.

actually removed by bioeroders may be even greater than suggested by Text-figure 11 because much of what is now seen as peloidal micrite may in fact originally have been reef framework, now changed beyond recognition by numerous generations of borers. This has been facilitated by the rapid synsedimentary cementation of fills of borings which allowed successive generations of borers to bore into previously excavated, refilled, and cemented borings. We thus do not think it is any exaggeration to claim the bioerosive processes can be responsible for removal of at least 50 per cent of the primary framework in some parts of the reef.

Although dwelling-borings were responsible for the great bulk of bioerosion that went on in the reefs, local evidence of grazing bioerosion is provided by rare bundles of scrape-marks on the inner faces of a few of the *Plicatula* (Pl. 3, fig. 6). These appear to be confined to the regions of the adductor muscle scars, either because decaying muscle tissue that attracted small scavengers lingered here, or perhaps because the myostracal aragonite was softer than the adjacent cross-lamellar aragonite and thus was more easily scratched.



TEXT-FIG. 11. Volumes of reef framework removed by small and large (bivalve) borings in the most heavily bored areas of the reef (reef edge). Data obtained by point counting on acetate peels from several different reefs.

EVOLUTIONARY AND ECOLOGICAL SIGNIFICANCE OF THE PORTLAND REEFS

Apart from rudist reefs, bivalve-dominated reefs are rare in the Mesozoic and restricted to comparatively small structures. The ?terquemiid bivalve *Placunopsis ostracina* Schlotheim built small domal or cushion-shaped reefs, up to several metres in width, in the Upper Muschelkalk of the German Basin (e.g. Bachmann 1979; Duringer 1985) and in the Ladinian of Provence, southeastern France (Brocard and Philip 1989) by cementation of numerous generations on top of one another, but only after the upper free valves had been removed. *Placunopsis* is the sole framebuilder in these reefs; encrusters are rare and consist of *Spirorbis*, foraminifers, and the bivalve *Enantiostreon* (Bachmann 1979). Borings in *Placunopsis* valves are confined to those of possible phoronids (*Calciroda kraichgoviae* Mayer, 1952 and *Talpina gruberi* Mayer, 1952). Usually they make up only a few per cent of the reef volume, although in rare cases up to 30 per cent of the framework volume has been destroyed (Bachmann 1979). The maker of *Trypanites*, which frequently occurs on the tops of the domes, postdates reef growth and was not part of the reef ecosystem.

Bivalve-dominated reefs also occur in the Kimmeridgian of the Lusitanian Basin, Portugal, and consist of structures, up to 2 m wide and 0·6–0·8 m high, composed of the oysters *Praeexogrya pustulosa* and *Nanogyra nana* (Fürsich 1981; Werner 1986). Reef growth was initiated in an apparently muddy lagoonal environment by overgrowth of large shells (e.g. *Isognomon*) lying on the sea floor. Apart from the principal framebuilder (*Praeexogyra pustulosa*), the accessory

framebuilders *Dorsoserpula* and *Juranomia* occur in low numbers. Nestlers (the bivalve *Arcomytilus*) are rare; vagile elements are more abundant and consist, above all, of a trochid gastropod and the echinoid *Pseudocidaris*. Reef destroyers are confined to occasional *Gastrochaenolites* and *Talpina*.

Reefs composed largely of bivalves become abundant in the Cretaceous, when various species of the oyster *Crassostrea* form, for example, patch reefs in enclosed bays on delta plains on the margin of the Western Interior Seaway (e.g. Kauffman 1967). *Crassostrea* is the only framebuilder in these reefs, associated with a varying number of encrusters (e.g. serpulids) and borers (acrothoracican barnacles, clionid sponges, and polydorid worms). Nestlers are confined to rare species of *Brachidontes*.

All these examples share a very low species diversity. They consist of only one or two framebuilders, and support a low number of subsidiary encrusters and borers. Their guild structures are comparable to those of most Mesozoic coral reefs as well as to the Portlandian reefs discussed here. The main difference is that each guild is occupied by very few members. Part of the reason is that these bivalve-dominated reefs grew in what appear to have been high stress environments. The marine fauna of the Muschelkalk is known to be impoverished due to the intermittent isolation of the German Basin. The Kimmeridgian *Praeexogyra-Nanogyra* patch reefs apparently grew in brackish bays and lagoons (Fürsich and Werner 1986), as did the Cretaceous *Crassostrea* patch reefs of the Western Interior Seaway (pers. observations; Fürsich 1994). The Portlandian patch reefs in contrast appear to have lived in a more fully marine environment and consequently exhibit a much higher diversity, though it is interesting to note the low diversity or complete absence of some major stenotopic groups such as bryozoans, brachiopods, corals, and echinoderms.

There is, however, another feature which distinguishes the Portland reefs not only from other bivalve-dominated reefs, but also from Jurassic coral reefs growing in comparable settings: the high diversity and numerical abundance of the reef destroyer guild. The Portland reefs are the oldest documented case where boring organisms can be shown to destroy such a very large part of the reef framework and associated cemented interstitial sediment. The diversity and abundance of borers differs drastically from that of shallow water calcisponge-coral reefs of the Alpine Triassic (e.g. Fürsich and Wendt 1977) where bioerosion is insignificant. Shallow water patch reefs of Jurassic epicontinental seas are bored, to a variable extent, by bivalves (*Gastrochaena*, *Lithophaga*), with few records of other boring taxa (e.g. Hallam 1975; Fürsich 1977; Palmer and Fürsich 1981; Fagerstrom 1978; Fürsich and Werner 1991). Although individual coral heads may be quite densely bored (e.g. Warme and McHuron 1978), the borers are, on the whole, far less conspicuous than in the Portland reefs. Part of an explanation is surely that extensive hard and solid substrates (shells of *Plicatula* and *Liostrea*; early diagenetically lithified matrix) facilitated boring much more than porous skeletons of, say, corals and calcareous sponges. Another part of the explanation involves the excellent preservation of borings facilitated by the early cementation of their fills and subsequent dissolution of the substrate. However, whereas this aspect probably enhanced the preservation potential of the various types of small borers (and thus records the original diversity of boring organisms more faithfully than in many other reefs: examples are *Spirichnus* and *Cunctichnus*), it did not have any influence on the abundance of borers and the percentage of bored reef framework. Still, these various aspects do not fully account for the importance of borers in the Portland reefs. It appears that these reefs document an evolutionary radiation of boring organisms that took place during the Jurassic. Most taxa of borers within the Portland reefs are known from earlier in the Jurassic or even Triassic (e.g. *Talpina*, *Rogerella*, *Gastrochaenolites*), but on the whole were less conspicuous at these earlier times. Bivalve borings have been made by four species within the Portland reefs in contrast to one or two taxa as recorded from most other Jurassic reefs. In addition, borings of clionid sponges (*Entobia*), the most abundant element among the smaller borings in the Portland reefs, are hardly known from older deposits. Published records are vague (e.g. Hallam 1975; Garcia *et al.* 1989) and may, in fact refer to borings of the haplosclerid sponge *Aka* which is not uncommon in the Mesozoic (Reitner and Keupp 1991), or even to other phyla. Apart from the abundance of borers in general, it is the abundance of *Entobia* in particular that gives the Portlandian patch reefs a modern aspect with respect to their reef destroyer guild; clionid sponges

are one of the most important destructive agents of present-day reefal and other hard calcareous substrates (e.g. Goreau and Hartman 1963; Neumann 1966; Rützler 1975; Bromley 1978).

The increasing importance and diversity of the destroyer guild during the Late Jurassic must have had far-reaching consequences for the reef ecosystem. Not only did it increase substantially the amount of reef debris, but it could also have promoted framebuilders with fast growth rates such as colonial scleractinian corals (e.g. Coates and Oliver 1973) within Mesozoic reefs.

SYSTEMATIC PALAEONTOLOGY

This study has recognized several new taxa: one new genus and species of bivalve; one new species of serpulid; two new ichnogenera and three new ichnospecies of boring. Several first occurrences of species or higher taxa are recorded for the British Portlandian. In addition, our observations cast further light on or disagree with some earlier assignments to the Portlandian fauna. These cases are discussed in this section.

Class BIVALVIA Linné, 1758
Family ARCIDAE Lamarck, 1809
Genus BARBATIA Gray, 1842
Subgenus BARBATIA Gray, 1842

Type species. Arca barbata Linné, 1758.

Barbatia (*Barbatia*) *bourgueti* Loriol, 1892

Plate 5, figure 2

Material. External mould of an articulated specimen, OUM J53657.

Description. Small, articulated shell, less than 10 mm in length, with prominent umbones situated in the anterior third of shell. Posterior umbonal ridge strong; anteriorly of it there exists a faint, shallow sulcus. Posterior demarcation of area in form of a thick, rounded rib. Surface ornament consisting of numerous closely-spaced radial ribs traversed by slightly less conspicuous comarginal growth lines resulting in a reticulate pattern. Radial ribs posteriorly of umbonal ridge rounded, stronger, and thicker than intervals between them. Hinge typical of *Barbatia*.

Remarks. Our specimens belong to a small species nestling in the reef framework. Smaller than de Loriol's specimen from the Oxfordian of the Swiss Jura (de Loriol 1892, p. 282, pl. 30, fig. 16), they exhibit a similar shape and ornamentation. *Barbatia kobyi* de Loriol (1892, p. 282, pl. 30, figs 17–19) from the Oxfordian of the Swiss Jura is also similar, but less elongate. Both species come from the same locality and may well represent different segments of the intraspecific range of a single species.

Family CUCULLAEIDAE Stewart, 1930
Genus CUCULLAEA Lamarck, 1801

Type species. Cucullaea auriculifera Lamarck, 1801.

Subgenus IDONEARCA Conrad, 1862

Type species. Cucullaea tippana Conrad, 1858.

Cucullaea (*Idonearca*) sp.

Remarks. The only specimen is an internal mould of a left valve showing a typical *Cucullaea* hinge. As the surface ornamentation is not known, a specific designation is not possible. The specimen resembles in overall shape *Cucullaea clathrata* Leckenby as figured by Lycett (1863, p. 44, pl. 39, fig. 4, 4*a*) from the Bathonian of England.

Family MYTILIDAE Rafinesque, 1815
Genus LITHOPHAGA Röding, 1798
Subgenus LITHOPHAGA Röding, 1798

Type species. Lithophaga mytiloides Röding, 1798.

Lithophaga (*Lithophaga*) *subcylindrica* (Buvignier, 1852)

Plate 5, figures 5–6

Material. Numerous complete internal moulds and, more rarely, external moulds (OUM J53661).

Remarks. Unlined borings of lithophagid bivalves, belonging to the trace fossil *Gastrochaenolites torpedo* Kelly and Bromley, 1984, are common in the reef facies (e.g. Pl. 6, fig. 6). Many of them contain shells which we refer to *Lithophaga* (*L.*) *subcylindrica* (Buvignier, 1852, p. 22, pl. 17, figs 20–21). This species has been regarded as a junior synonym of *L. inclusa* (Phillips, 1829) by Pisera (1987) who argued that Buvignier's specimens fall within the range of variation of a population of *L. inclusa* from the Upper Jurassic of Poland. We feel, however, that a more thorough revision of the group is needed before morphologically such widely differing taxa are synonymized. The Portlandian specimens have a straight dorsal and only a gently convex ventral margin compared to the strongly convex dorsal and ventral margins of typical *L. inclusa*.

Lithophaga sp. A

Plate 5, figure 8

Material. Two shell fragments (OUM J53662).

Remarks. Lithophaga sp. A differs from all other *Lithophaga* by displaying distinct radial ribs in the anterior of the shell which fade from the umbo to the ventral margin and disappear progressively in a posteroventral direction. The posterior half of one specimen and the posterior third of a second specimen are smooth except for conspicuous growth lines. Most likely *Lithophaga* sp. A represents a new species, but as only two incomplete specimens are available, we prefer an informal designation until more material becomes available.

Genus MODIOLUS Lamarck, 1799
Subgenus MODIOLUS Lamarck, 1799

Type species. Mytilus modiolus Linné, 1758.

EXPLANATION OF PLATE 5

Figs 1, 9. *Gastrochaenopsis recondita* (Phillips). 1, OUM J53656; latex cast of external mould of articulated specimen; dorsal view; × 10. 9, OUM J53663; internal mould of articulated specimen; right valve view; × 7.

Fig. 2. *Barbatia* (*Barbatia*) *bourgueti* de Loriol. OUM J53657; latex cast of external mould of articulated specimen; dorsal view; × 8.

Figs 3–4, 7. *Hiatella* (*Pseudosaxicava*) *phaseolus* (Eudes-Deslongchamps). 3, OUM J53658; internal mould of articulated specimen; right valve view; × 8. 4, 7, latex casts of external moulds of right valves; 4, OUM J53659; × 8; 7, OUM J53660; × 12.

Figs 5–6. *Lithophaga* (*Lithophaga*) *subcylindrica* (Buvignier). OUM J53661; 5, dorsal view; 6, left valve view of articulated specimen; × 3.

Fig. 8. *Lithophaga* sp. A. OUM J53662; articulated specimen, right valve view; × 6.

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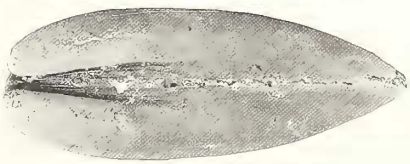
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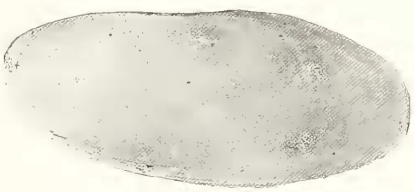
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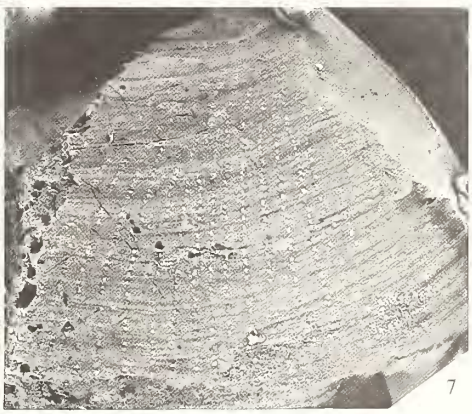
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FÜRSICH *et al.*, Portland reef bivalves

Modiolus (*Modiolus*) sp.

Material. Fourteen whole and broken specimens (OUM J53707).

Remarks. Small nestling species characterized by an extremely long hinge line, and well rounded posterior end. Similar in shape to *M. jurensis*, but the latter is much larger in size.

Family PLICATULIDAE Watson, 1930
Genus PLICATULA Lamarck, 1801

Type species. Spondylus plicatus Linné, 1758.

Plicatula damoni Cox, 1937

Plate 3, figure 4

Material. Several hundred internal moulds (OUM J53652).

Remarks. Cox (1929, p. 164, pl. 4, figs 3–4) described specimens of *Plicatula* from the Late Jurassic of the Isle of Portland as *P. lamellosa* n. sp., but later on (Cox 1937) renamed it *P. damoni*, as *P. lamellosa* was preoccupied by a species from the Cretaceous of Russia.

As our material consists of internal moulds only, little can be said about the relationship of *P. damoni* to other species of *Plicatula*. Size ranges up to a length of *c.* 45 mm; shape is extremely variable as a result of growth in confined spaces in the reef framework.

Family GASTROCHAENIDAE Gray, 1840
Genus GASTROCHAENOPSIS Chavan, 1952

Type species. Gastrochaena unicostata Eudes-Deslongchamps, 1838.

Gastrochaenopsis recondita (Phillips, 1829)

Plate 5, figures 1, 9

Material. Fifteen specimens, both internal and external moulds (OUM J53656, J53663).

Remarks. Pholas recondita Phillips (1829, pl. 3, fig. 19) was put into the genus *Spengleria* Tryon, 1862, by Pisera (1987) who regarded *Gastrochaenopsis* as a junior synonym of the latter. Both

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EXPLANATION OF PLATE 6

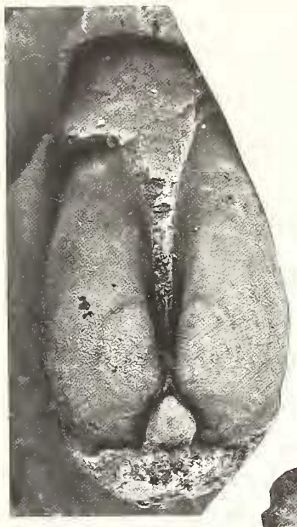
Figs 1–5, 7. *Carterochaena pulcherrima* gen. et sp. nov. 1, OUM J53664, paratype; internal mould of articulated specimen, dorsal view; ×9. 2, OUM J53665, holotype; internal mould of articulated specimen, dorsal view; ×9. 3, OUM J53666, paratype; internal mould of right valve; ×7. 4, OUM J53667; internal mould of articulated specimen in boring, left valve view; ×9. 5, OUM J53688; internal mould of articulated specimen; dorsal view showing cavities produced by the dissolved shell material of valves and accessory plate; ×25. 7, OUM J53669; side view of internal mould of anterior region of articulated specimen showing position of accessory plate; ×25.

Fig. 6. *Gastrochaenolites torpedo* Kelly and Bromley. OUM J53670; ×2.

Fig. 8. *Caulostrepsis cretacea* (Voigt). OUM J53671; ×7·5.

Fig. 9. *Rogerella pattei* (Saint-Seine). OUM J53672; ×6.

Fig. 10. *Cunctichnus probans* ichnogen. et ichnosp. nov. OUM J53673, holotype; ×2.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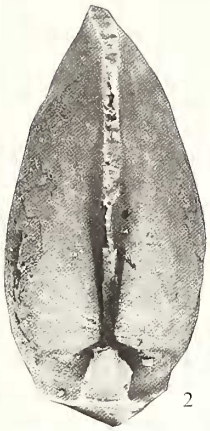
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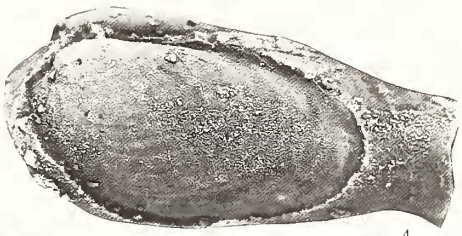
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FÜRSICH *et al.*, Portland reef biota

Gastrochaenopsis and *Spengleria* are characterized by a triangular area running from the umbo to the truncated posterior end. This area is separated from the rest of the shell by strongly raised growth lamellae. In *Spengleria*, this area is bordered ventrally by a distinct furrow which is absent from *Gastrochaenopsis*. The latter genus is therefore kept separate from *Spengleria*.

The Portland specimens agree well with the material described from the Corallian (Oxfordian) by Arkell (1933, p. 313, pl. 43, figs 1–4) and from the Oxfordian-Kimmeridgian of Poland by Pisera (1987, p. 93, pl. 38, figs 1–3, text-figs 7–9). *Gastrochaenopsis recondita* is more elongate than species of *Gastrochaena* but exhibits, like the latter, a distinct anteroventral pedal gape. Internal moulds of *G. recondita* do not show a raised area, but have a rounded posteroventrally-directed umbonal carina followed dorsally by a wide shallow depression. This depression is bordered dorsally by a second, slightly less conspicuous umbonal carina running to the posterodorsal margin. The elevated posterior area of the shell, so characteristic of the genus, is therefore exclusively produced by the strongly raised growth lamellae and is not seen on internal moulds.

On some of the internal moulds, a wide pallial sinus of intermediate depth has been observed.

The boring of the species exhibits a thin calcareous lining which is well preserved and was not, therefore, originally aragonite. According to its shape, the boring can be accommodated in *Gastrochaenolites dijugus* Kelly and Bromley, 1984.

?Family GASTROCHAENIDAE Gray, 1840
Genus CARTEROCHAENA gen. nov.

Derivation of name. After J. G. Carter, from *Gastrochaena*.

Type species. Carterochaena pulcherrima sp. nov.

Diagnosis. Gastrochaena-like bivalve with accessory plate situated anterior of umbones between the two valves.

Remarks. Carterochaena is identical to *Gastrochaena* in outline and differs solely by the presence of the accessory plate. So far, accessory plates are not known in members of the Gastrochaenidae, but are characteristic of the family Pholadidae. Despite this fact we prefer to group *Carterochaena* – with reservation – with the Gastrochaenidae because: (a) none of the other characteristic features of members of the Pholadidae, such as apophyses, callum, umbonal ventral rib, radial ornament, etc., are present; and (b) the shape of the valves so strikingly resembles that of *Gastrochaena* that without the accessory plate, the specimens would undoubtedly be referred to the latter genus.

Carterochaena pulcherrima sp. nov.

Plate 6, figures 1–5, 7

Derivation of name. Superlative of *pulcher* (Latin), meaning 'beautiful'.

Type series. Holotype: OUM J53665 (Pl. 6, fig. 2); paratypes: OUM J53664, J53666, J53667 (Pl. 6, figs 1, 3, 4 respectively).

Material. 110 predominantly internal moulds (OUM J53664–J53669).

Diagnosis. Elongate-ovate gastrochaenid with strongly reflected anteroventral margin and elongate to triangular-ovate accessory plate between the two valves anterior of umbones.

Dimensions of internal moulds (in mm; L, length; H, height).

L	H	L	H	L	H
8·0	4·6	6·4	4·3	6·8	4·0
11·5	—	6·0	3·8	8·5	5·4
8·2	5·2	8·0	4·6	7·5	4·5
4·4	2·5	7·5	4·6	6·2	3·8
7·8	4·6	7·5	4·5	4·2	2·8
5·2	3·1	7·7	4·6	5·1	3·7
6·5	4·4	7·0	4·7	6·6	4·2
7·5	4·3	6·2	4·0	6·7	3·9
8·4	5·0	7·5	4·1	8·8	4·4
6·1	3·0	6·1	3·9		

Description. Small (on average 5–10 mm long), moderately inflated shell. Umbones prosogyrate, situated close to the anterior end. Dorsal margin straight, grading into well rounded posterior margin. Ventral margin faintly convex posteriorly, but strongly reflected anteriorly resulting in a straight to faintly concave anterior margin and a wide anteroventral pedal gape. Anterodorsal shell margin slightly reflected along the plane of commissure. Anterior adductor muscle scar situated in the anterodorsal corner of the valve; posterior adductor scar somewhat larger. Pallial sinus wide and deep. Shell ornamented with numerous fine, faintly rugose growth lines.

Accessory plate elongate ovate to rounded triangular in shape with a beak-like end pointing in the direction of the umbones. The accessory plate closely fits between the upturned anterodorsal shell margins. Judging from the cavity space between internal and external moulds (Pl. 6, fig. 5), the thickness of the plate was at least twice that of the valves.

Remarks. The main diagnostic feature of *Carterochaena pulcherrima* is the presence of a thick accessory plate. In the Pholadidae such plates, when situated anteriorly of the umbones (e.g. protoplax), serve to protect the anterior adductor muscle which inserts on the reflected dorsal margin. The anterior adductor muscle inserts very closely to the anterodorsal margin and transverses right behind the pedal gape in pholadids and *C. pulcherrima*, and a similar function of the accessory plate seems likely. However, the facts that the plate is much thicker than the rest of the shell and that it is positioned at the anterodorsal end of shell and projecting slightly beyond it, suggest that it may well have aided the boring process by mechanically abrading hard substrates that had been chemically weakened. Any shell material that was lost during this process could have been replaced by addition of new layers on the inside of the plate.

C. pulcherrima occurs in *Gastrochaenolites dijugus* Kelly and Bromley, 1984, flask-shaped borings characterized by a restricted neck region with a figure of eight cross-section. The boring exhibits a thin calcareous lining which, as in the case of *G. recondita*, was not aragonitic.

Genus HIATELLA Bosc, 1801

Type species. *Hiatella monoperta* Bosc, 1801.

Subgenus PSEUDOSAXICAVA Chavan, 1952

Type species. *Pseudosaxicava bernardi* Chavan, 1952.

Hiatella (*Pseudosaxicava*) *phaseolus* (Eudes-Deslongchamps, 1838)

Plate 5, figures 3–4, 7

Material. Sixty five specimens, both internal and external moulds and casts (OUM J53658–J53660).

Remarks. The Portlandian specimens were described as *'Arca' foetida* n. sp. by Cox (1929, p. 140, pl. 1, figs 2–3). Kelly (1980) placed *'A.' foetida* with *Hiatella* (*Pseudosaxicava*) and, later (Kelly 1985, p. 172, fig. 1), regarded it as a junior synonym of *Hiatella* (*Pseudosaxicava*) *arcadiformis* (Keeping, 1883). Pisera (1987, p. 90, pl. 37, figs 1–4, text-figs 5–6) regarded *H.* (*Pseudosaxicava*) *arcadiformis* as a junior synonym of *Saxicava phaseolus* Eudes-Deslongchamps (1838, p. 227, pl. 9, figs 25–26, 33–34), arguing that the different species represent only intraspecific variants of a morphologically very plastic species. Pisera's view is followed here.

This highly variable species, up to 15 mm in length (average 6–8 mm), is characterized by a subrectangular outline and a strong posterior carina running to the posteroventral shell margin. A second, less conspicuous carina runs from the umbo to the posterodorsal margin. Silicon rubber casts of external moulds reveal faint growth lines and an ornament of radially arranged lines of minute pustules. This ornament extends across most of the shell (Pl. 5, fig. 7) or else is restricted to patches on the flank of the valves (e.g. Pl. 5, fig. 4). Such pustules may correspond to periostracal spikes (see also Pisera 1987). Clavulate spines also occur at regularly spaced intervals on both carinae. Some internal moulds exhibit large adductor muscle scars and a wide, moderately deep pallial sinus (Pl. 5, fig. 3).

The great variability of the species is largely a result of its nestling habit. *Hiatella* (*Pseudosaxicava*) *phaseolus* was found, above all, in *Gastrochaenolites torpedo* (which, in addition, often contained valves of the borer *Lithophaga*) and in *G. dijugus*.

Phylum ANNELIDA Lamarck, 1809
Family SERPULIDAE Burmeister, 1837
Genus SERPULA Linné, 1758

Type species. Tubus vermicularis Ellis, 1755.

Subgenus CYCLOSERPULA Parsch, 1956

Type species. Serpula flaccida Goldfuss, 1831.

Serpula (*Cycloserpula*) *striatissima* sp. nov.

Plate 3, figure 3

Derivation of name. Superlative of *striatus* (Latin), meaning 'striped'.

Type series. Holotype: OUM J53653.

Material. Numerous external moulds embedded into the surface of internal moulds of *Plicatula*.

Diagnosis. Serpula with round cross-section and seven axial riblets.

Description. Small, encrusting serpulid, 0·3–0·7 mm in diameter, with irregular, winding course. Usually, the tubes disappear into the substrate after having meandered across the surface for most of their length which suggests that the youngermost parts of the tubes became detached from the substrate and grew away from it.

Cross-section round. Surface ornament of seven axial riblets crossed by numerous fine growth lines, producing a slightly reticulate pattern, and more widely spaced annulae.

Remarks. Despite the large number of serpulid species known from the Jurassic the present specimens do not match any of them. They are therefore accommodated in the new species *striatissima* within the form subgenus *Cycloserpula*.

ICHNOTAXA

Ichnogenus ARACHNOSTEGA Bertling, 1992

Type ichnospecies. Arachnostega gastrochaenae Bertling, 1992.

Arachnostega gastrochaenae Bertling, 1992

Plate 3, figures 1–2, 4

Material. Numerous specimens in fills of bivalves (OUM J53650–J53652).

Description. Irregularly ramifying and anastomosing burrows with circular to oval cross-section. Preserved as negative reliefs or calcite-filled endoreliefs at the surface of internal moulds of *Plicatula damoni* or other bivalves such as *Lithophaga*. The burrows are roughly cylindrical, branch frequently but at irregular intervals, whereby branches join up to form networks. Several 'ontogenetic' stages are present: the tunnels of the smallest networks are around 0·03 mm in diameter, those of the largest networks 1·5 mm. Average tunnel diameter is 0·3–0·5 mm. The diameter of individual networks remains fairly constant, but networks of different sizes are connected with each other. Also, parts of smaller networks are commonly seen to branch off (or join?) larger ones.

Remarks. The burrows closely resemble those recently described from internal moulds of molluscs from Late Jurassic reefs of northern Germany (Bertling 1992). Similar traces were recorded by Reineck (1980) from the tidal flats of the North Sea, there made by the polychaetes *Heteromastus* and *Nereis* in stiff sediment fills of the bivalve *Mya arenaria*. Accordingly, Bertling (1992) assumed errant polychaetes to be the producers of the Jurassic burrow systems.

A. gastrochaenae is a ubiquitous trace in internal moulds of bivalves in the Portlandian reefs. Very likely, their producers preferred internal sediments as these might have contained a higher concentration of bacteria and other organic matter produced by the decay of the original soft parts. Moreover the Recent *Heteromastus filiformis* is known to live in oxygen-poor sediments (e.g. Dörjes 1978, p. 134) and thus is adapted to exploit the niche of sediment-filled shells. However, it is unlikely that the producers of *A. gastrochaenae* were confined to the environments from which the trace is known so far. It is the low preservation potential of such traces outside the shell-protected microhabitat, especially their disappearance during compaction, that creates such a specific distribution pattern.

As Bertling (1992) suggested, the different-sized meshworks most likely represent different age groups within the population of the producer. Such burrows are built in such a short time that no size increase due to growth of the producer can be usually detected.

Ichnogenus CAULOSTREPSIS Clarke, 1908

Type ichnospecies. Caulostrepsis taeniola Clarke, 1908.

Caulostrepsis cretacea (Voigt, 1971)

Plate 6, figure 8

Material. More than twenty five natural casts in dissolved *Plicatula* shells (OUM J53671).

Description. Pouch-like flattened boring, 5–12 mm in length with a flat-oval cross-section (for terminology see Bromley and d'Alessandro 1983, fig. 2). Near point of origination, the width-height ratio is about two and

increases up to four near the vertex. Course of boring straight to sometimes sinuous or twisted in a step-like fashion. No vane developed, but an axial depression is commonly present.

Remarks. Bromley and d'Alessandro (1983) discussed several ichnospecies of *Caulostrepsis* in detail. Our material fits best the description of *C. cretacea*, although an axial depression (not corresponding to a vane) is far more common and pronounced than in the material described by Bromley and d'Alessandro (1983). *C. taenida* Clarke, 1908 differs by possessing a distinct vane and a corresponding dumb-bell cross-section.

The producer of the borings was most likely a polychaete (compare Recent borings of *Polydora* and *Dodecaceria*).

Ichnogenus CUNCTICHNUS ichnogen. nov.

Derivation of name. cunctare (Latin), meaning 'hesitate' (after the behaviour pattern of the trace fossil producer); *ichnos* (Greek), meaning 'trace'.

Type ichnospecies. Cunctichnus probans ichnosp. nov.

Diagnosis. Cylindrical borings in shells, arcuate to highly sinuous or planispiral, with thin, short, tapering side-branches at points where the tubes abruptly change direction.

Cunctichnus probans ichnosp. nov.

Plate 6, figure 10; Text-figure 12A

Derivation of name. (Latin) *probare*, meaning 'to probe'.

Type series. Holotype: OUM J53673.

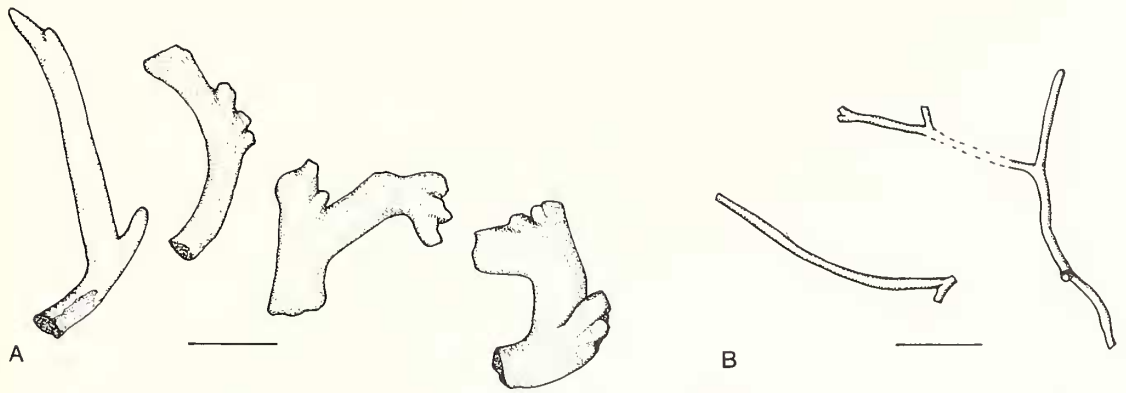
Material. More than 20 specimens occurring as natural casts in dissolved *Plicatula* shells.

Diagnosis. As for ichnogenus.

Description. Cylindrical tunnels of a constant diameter ranging from 0·8 to 4 mm in different specimens. Cross-section circular to slightly elliptical in the plane of boring. Borings occur as casts of tunnels in dissolved shells of *Plicatula damoni*. Course of tunnels arcuate, planispiral, or highly sinuous, defined by shape of available substrate. Where the arcuate tunnel casts approach the margin of the host substrate, thin and short side-branches with a tapering or blunt end, often not more than 1–2 mm in length and less than 1 mm in diameter, extend either at some angle from or in continuation of the main shaft. The main shaft then continues at an angle (sometimes more than 90°) from the original direction until the margin of the host substrate is encountered somewhere else. The casts never cross each other, very rarely touch each other, but often run parallel to each other with less than 0·1 mm distance between them. The cross-section of the short side-branches varies from circular to distinctly flattened. Often, two or more side-branches occur side by side.

Elongate-oval bulges, 0·1–0·2 mm across, arranged parallel to the long axis of the cylinder, were observed in one specimen. They correspond to shallow scoops on the walls of the boring and most likely represent individual phases of the excavation process.

Remarks. There can be little doubt that the course of the boring is determined to a large extent by the shape of the substrate. The side-branches represent probing tunnels through which the organism was able to sense the edge of the substrate. This, as well as the fact that the borings do not cut themselves but may run closely parallel to an earlier limb, points to a negative thigmotactic



TEXT-FIG. 12. Sketches of branching patterns in new ichnospecies of borings from the Portland reefs. A, *Cunctichnus probans* ichnogen. et ichnosp. nov. showing thin and short side branches where animal has approached the outer edge of the *Plicatula* substrate, has withdrawn a couple of millimetres, and has set off again in a different direction in order to remain within the shell; scale-bar is 5 mm. B, branching in *Talpina bromleyi* ichnosp. nov.; scale-bar is 2 mm.

behaviour of the producer. The thin side-branches suggest that the first step in boring was a short, thin exploratory shaft which, when the substrate proved satisfactory, was enlarged to its final size. This behaviour minimized energy expenditure in case the adopted direction had to be aborted. The probing tunnels indicate that the producer was an animal with a proboscis. A sipunculid origin of the boring is therefore likely.

Possibly a somewhat similar behaviour is displayed by some *Vermiforichnus clarkei* Cameron, 1969, from the Devonian Hamilton Group of New York State when these tunnels reach the limits of their brachiopod host substrates (e.g. Häntzschel 1975, fig. 82–1*a*).

Ichnogenus ENTOBIA Bronn, 1838

Type ichnospecies. Entobia cretacea Portlock, 1843.

Entobia cervicornis ichnosp. nov.

Plate 7, figures 1–2, 4

Derivation of name. (Latin) *cervus*, meaning 'deer'; (Latin) *cornua*, meaning 'antlers'.

Type series. Holotype: OUM J53674 (Pl. 7, fig. 1); paratypes: OUM J53675–J53676 (Pl. 7, figs 2, 4).

Material. Numerous specimens, preserved as natural casts in dissolved *Plicatula* shells.

Diagnosis. Non-camerate *Entobia* forming an irregular boxwork in growth phase C (*sensu* Bromley and d'Alessandro 1984). Phase A represented by long slender tubules grading into thicker, antler-shaped cylindrical tubes of growth phase B. Phases D–E not developed. Typical chip micro-ornament, as seen in most clionid borings, is absent.

Description. Anastomosing *Entobia* of widely differing diameter. Long, slender tubules (exploratory threads) of phase A (for terminology see Bromley and d'Alessandro 1984) widespread, around 50 μm in diameter

(Pl. 7, fig. 2). Growth phase B is also very common and represented by antler-shaped cylindrical tubes, 100–300 μm in diameter, branching in three dimensions. The final developmental stage is phase C in which galleries, subcylindrical to oval in cross-section, connect to form an irregular anastomosing boxwork. At branching points, several branches often take off, usually parallel to laminae of the microstructure of the host shell. Diameter of galleries varies between 350 and 850 μm. Apertures rarely observed, around 250 μm in diameter.

Remarks. In shape and branching pattern, this ubiquitous boring is similar to *Entobia megastoma* (Fischer, 1868) as described by Bromley and d'Alessandro (1984). Major differences are the distinctly smaller size of *E. cervicornis* and the lack of developmental stage D. Thus, the boxwork of *E. cervicornis* never reaches the stage where most of the substrate has been removed and only thin columns are left between the galleries as is the case in *E. megastoma*. The oval cross-section of some phase C galleries probably results from the parallel arrangement of these galleries to the laminae of the shell microstructure.

Like other species of *Entobia*, *E. cervicornis* can be attributed to the boring activity of clionid sponges.

Ichnogenus IRAMENA Boekschoten, 1970

Type ichnospecies. Iramena danica Boekschoten, 1970.

Iramena ichnosp.

Plate 4, figures 2–4

Material. Several colonies in two shells of *Liostrea expansa*. Three specimens preserved as natural internal moulds (OUM J53681–J53683).

Remarks. The ichnogenus *Iramena* was erected by Boekschoten (1970, p. 45) for bryozoan borings with round to reniform apertures of zooids and an irregular tunnel network representing stolons.

Borings of bryozoans are claimed by both bryozoologists and ichnologists. As no parts of the producing bryozoans are left after their decay, the boring has to be treated as a trace fossil, although it apparently accurately reflects the shape of the organism (see discussion in Häntzschel 1975, p. W136; cf. Pohowsky 1974).

Iramena is relatively rare in the Portland reefs. The short, vertical to oblique tunnels (zooids), which are arranged at right angles to, and alternately along the tunnel network (stolons), are connected to it by thin tunnels (peduncles). Depending on the degree of erosion of the shell surface, the zooidal tunnels are round to tear-shaped in cross-section. Their apertures are circular and measure 30–35 μm in diameter. The zooidal tunnels extend, slightly inclined to faintly curved, about 100–150 μm into the substrate. Their cross-section is oval and they exhibit a tapering end.

The shape of the borings corresponds well to that of the ctenostome bryozoan genus *Penetrantia* Silén, 1946, which is characterized by pedunculate zooids orientated more or less vertically in the

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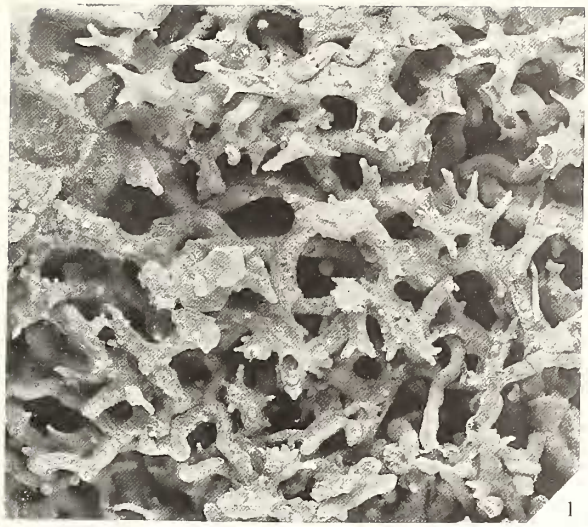
EXPLANATION OF PLATE 7

Figs 1–2, 4. *Entobia cervicornis* ichnosp. nov. 1. OUM J53674, holotype; growth phases B and C; × 5. 2, OUM J53675, paratype; growth phases A and B; × 5. 4, OUM J53676, paratype; growth phase B; × 5.

Figs 3, 6. *Spirichnus spiralis* ichnogen. et ichnosp. nov. 3, OUM J53677, paratype; × 6. 6, OUM J53678, holotype; × 6.

Fig. 5. *Talpina bromleyi* ichnosp. nov. OUM J53679, holotype; × 7·5.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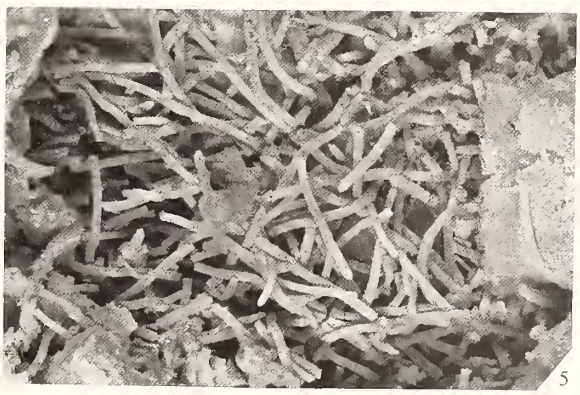
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FÜRSICH *et al.*, *Entobia*, *Spirichnus*, *Talpina*

substrate (Pohowsky 1978). The genus was known previously only from the mid-Cretaceous to the Recent. Its occurrence in the Portland reefs extends its record back to the Late Jurassic.

The internal moulds represent a new species of *Penetrantia*, differing distinctly from those described so far.

Ichnogenus ROGERELLA Saint-Saine, 1951

Type ichnospecies. Rogerella lecontrei Saint-Saine, 1951.

Rogerella pattei (Saint-Seine, 1954)

Plate 6, figure 9

Material. Numerous natural casts in dissolved *Plicatula* shells (OUM J53672).

Description. Elongate to short, pouch-shaped borings with expanded and flattened anterior. Maximum width 1·5–1·7 mm; length 2·7–3 mm.

Remarks. Several ichnogenera such as *Rogerella* Saint-Seine, 1951, *Simonizapfes* Codez and Saint-Seine, 1958, and *Zapfella* Saint-Seine, 1954 exist for sac- to pouch-shaped borings with slit-like openings which are made by acrothoracican barnacles. We agree with Bromley and d'Alessandro (1987) that one ichnogenus is sufficient to accommodate most cirriped borings. The Portland material can therefore be referred to the earliest-named of these available ichnogenera, *Rogerella*. There is no significant difference between our material and *Rogerella pattei* (Saint-Seine, 1954, p. 448) to which it is therefore referred.

On *Plicatula damoni*, *R. pattei* usually occurs in clusters of three to twelve individuals.

Ichnogenus SPIRICHNUS ichnogen. nov.

Derivation of name. (Latin) *spira*, meaning 'anything coiled'; (Greek) *ichnos*, meaning 'trace'.

Type ichnospecies. Spirichnus spiralis ichnosp. nov.

Diagnosis. Spirally-coiled cylindrical spiral borings.

Spirichnus spiralis ichnosp. nov.

Plate 7, figures 3, 6

Derivation of name. (Latin) *spiralis*, meaning 'spiral'.

Type series. Holotype: OUM J53678 (Pl. 7, fig. 6); paratype: OUM J53677 (Pl. 7, fig. 3).

Material. Numerous specimens and fragments of varying length.

Diagnosis. Cylindrical, irregularly spirally-coiled borings of 0·5 mm in diameter, branching at highly irregular intervals.

Description. Cylindrical casts of constant diameter (0·5 mm) which are spirally coiled. Coils usually tight, but looser at irregular intervals. Where the spiral coils are closely set, the cross-section of the casts is not strictly circular, but appears to have a bulge towards the coiling axis. Several specimens therefore show a vane-like development.

Branching occurs commonly, but at highly irregular intervals. Unbranched cylinders up to 23 mm in length have been observed, but also specimens where Y-shaped branching occurred every 2–3 mm. The branching does not occur in a plane, but produces a three-dimensional network. Density of *Spirichnus spiralis* is very high in some specimens resulting in a dense boxwork of cylindrical casts. In other specimens, *S. spiralis* appear to be confined to certain shell layers and the resulting network forms a plane with the spiral axes running parallel to it. In these cases, the spiral coils are often compressed laterally, apparently due to lack of usable space.

Remarks. No comparable borings are known from the literature. *Spirichnus spiralis* resembles *Meandropolydora barocca* Bromley and d'Alessandro (1987, p. 386, pl. 40, figs 1–3; pl. 43, fig. 3; pl. 44, figs 1–2, 5; pl. 47, fig. 1; pl. 48, fig. 4; text-figs 12–14) from the Pleistocene of southern Italy in cases where the bulged circular cross-section hints at the presence of a vane. However, pouches are never developed and *S. spiralis* must therefore be kept as a separate ichnotaxon. Its producer remains unknown, but probably belongs to one of the several phyla of 'worms'.

Ichnogenus TALPINA Hagenow, 1840

Type ichnospecies. Talpina ramosa Hagenow, 1840.

Talpina bromleyi ichnosp. nov.

Plate 7, figure 5; Text-figure 12B

Derivation of name. After R. G. Bromley.

Type series. Holotype: OUM J53679 (Pl. 7, fig. 5).

Material. Several hundred specimens on internal moulds of *Plicatula.*

Diagnosis. Straight to gently curved branched cylindrical borings, 0·25 mm in diameter. Distance between branching points much longer than in other species of *Talpina.*

Description. Straight to gently curved cylindrical casts, running parallel and close to the surface of the original shell. Diameter of casts 0·25 mm. Branching occurs, but is far less common than in other ichnospecies of *Talpina.* Branches usually take off from the convexly curved sides of borings. No anastomosing was observed. Where density of boring is low, the galleries run close to the surface of the shell; in densely bored shells, the galleries extend to lower levels, 1–2 mm below the surface. Rarely, shallow, simple or combined U-tubes from which horizontal galleries branch off connect to the surface. Where density of boring is very high, frequently two or three galleries can be observed to run parallel to each other for several millimetres, separated from each other by only a few microns, but never touching. *T. bromleyi* never cut each other, but cross over or under an already existing tunnel.

Remarks. Diameter of borings, branching pattern, and arrangement of galleries with respect to the surface are typical of *Talpina.* The very similar ichnogenus *Conchotrema* differs by having a much more irregular network and by displaying anastomosis. *T. bromleyi* differs from other ichnospecies of *Talpina* (*T. ramosa* Hagenow, 1840, *T. hirsuta* Voigt, 1975, *T. eduliformis* Quenstedt, 1858, *T. gruberi* Mayer, 1952, and *T. annulata* Voigt, 1975) by displaying a markedly lower frequency of branching. The relatively great depth of penetration seen in densely bored *Plicatula* shells is obviously a result of crowding. The apertures of the lowest networks may possibly have connected to abandoned shallower galleries and not necessarily straight to the surface.

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FRANZ T. FÜRSICH
Institut für Paläontologie
Universität Würzburg
Pleicherwall 1
D-97070 Würzburg, Germany

TIMOTHY J. PALMER
KAY L. GOODYEAR
Institute of Earth Studies
University of Wales, Aberystwyth
Aberystwyth, Dyfed SY23 3DB, UK

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